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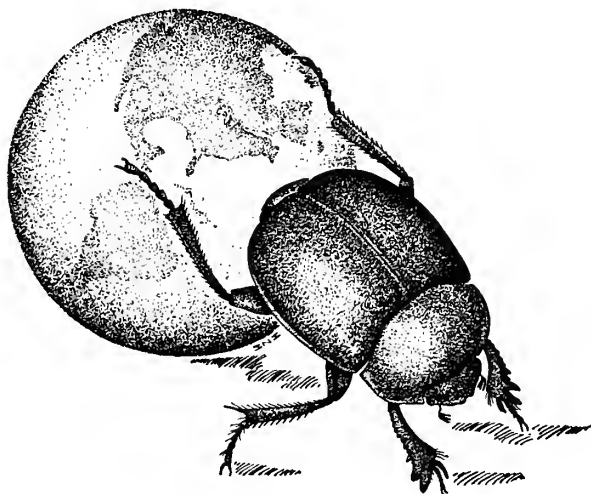
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**A PHYLOGENETIC ANALYSIS AND RECLASSIFICATION
OF THE GENERA OF THE *POCOCERA* COMPLEX
(LEPIDOPTERA: PYRALIDAE: EPIPASCHIIINAE)**

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Abstract.—Based on a worldwide survey of representatives of epipaschiine genera, a monophyletic subset is identified and designated the *Pococera* complex. Its monophyly is defended by a prominent saccus in the male genitalia and a long, narrow ductus bursae in the female genitalia. The complex contains approximately 300 species that are restricted in distribution to the Western Hemisphere. This phylogenetic study of the complex establishes its monophyly, re-examines the genera included, establishes their monophyly, and estimates their relationships.

The cladistic analysis is based on 22 taxa and 65 characters of the adult head, genitalia, and wings. *Lacalma* Janse and *Macalla* Walker are used as outgroups. The PHYSYS program generated three equally parsimonious trees with a length of 144 and consistency index 0.52. The stability of the estimated trees were tested with successive weighting and sequential removal of taxa. The tests showed the position of the root to be somewhat uncertain. Nevertheless, the topology of the estimated trees is shown to be stable in most manipulations despite the fact that most of the groupings are supported by very few characters.

A taxonomic synopsis presents the results of the examination and the definition of the genera as monophyletic. Twenty-two genera of the *Pococera* complex are diagnosed and six new genera are described. Representatives of each genus are illustrated by line drawings and photographs. Larval host use patterns are briefly reviewed. A nomenclatural summary is provided, including taxa to be removed from the Epipaschiinae.

The Epipaschiinae are one of five subfamilies currently placed in the Pyralidae (Solis and Mitter, 1992). The monophyly of the Pyraloidea and the Pyralidae are well supported in the literature (Solis and Mitter, 1992) and is not in dispute. The monophyly of the Epipaschiinae was established and discussed previously (Solis and Mitter, 1992), but relationships within this subfamily are not well understood. The Epipaschiinae historically include approximately five hundred species that are primarily pan-tropical in distribution. They occur from the northern periphery of Australia north into the Oriental Region, including temperate China, and to the southern limits of the Palearctic. They also are found south of the Sahara to South Africa and in the Western Hemisphere from the eastern temperate forests to northern Argentina.

Information is limited on the life history and immature stages of the Epipaschiinae. The morphology of the immatures is not well known (Allyson, 1977; Passoa, 1985). The larvae are known to be leafrollers, leaf tiers, and leafminers. Some species are believed to be host specific, for example, *Epipaschia superatalis* Clemens on poison ivy. Other species, such as *Phidotricha erigens* Ragonot, have been reared on a wide variety of hosts, including loquat, tamarind, lima beans, sorghum, and corn. As

illustrated by hosts of *P. erigens*, some species in the tropics are economically important.

The Epipaschiinae have been the subject of very few comprehensive morphological, and no modern phylogenetic, studies. Hampson (1896) was the first to study the genera on a worldwide basis; he used wing venation and external characters of the head. Janse (1931) conducted a survey of the genera and was the first to use male genitalia and secondary sexual characters of the head after removing the scales. He often investigated only one specimen of one species, the type species, or a species he had access to, and at times depended on opinions about type species by other taxonomists. He delineated genera based on male characters of the genitalia, head, and wings. The lack of modern, comprehensive studies in the Epipaschiinae is evident in a list of species (see Nomenclatural Summary) which, during the course of this study, were found to belong in other subfamilies.

To delineate major monophyletic groups, a survey of the major genera of the Epipaschiinae was conducted. First, the exact size and content of the Epipaschiinae on a worldwide basis were determined by developing lists of genera and species for the Western Hemisphere and for those found elsewhere. Fletcher and Nye (1984) listed fifty-four genera and I found 385 species outside the Western Hemisphere (Solis, in press). In the Western Hemisphere fifty-eight genera were listed by Fletcher and Nye (1984) and I found 370 species.

Second, representative specimens of genera were dissected and studied. From the Western Hemisphere a male and female specimen of the type species of forty-five genera were dissected. Other species examined in each genus are listed in the generic synopsis. Outside the Western Hemisphere almost all type species were seen and at least one male and one female of each type species of twelve major genera were dissected. In the larger genera examples of more than one species was dissected, and some species were dissected whose generic affinity was not known.

The most clearly evident monophyletic group identified by this survey was a large set of genera that is found only in the Western Hemisphere and is here termed the *Pococera* complex. This is not to be confused with Pococerinae, a synonym of the Epipaschiinae. This complex comprises forty-seven generic names and approximately three hundred specific names. The complex includes several large and economically important genera such as *Pococera* Zeller and *Phidotricha* Ragonot. The complex is named after *Pococera* because the genus is the largest occurring in North America and is commonly associated with the subfamily name by lepidopterists.

This study is a generic re-classification and phylogenetic analysis of the *Pococera* complex based on a morphological study of the adults, and it will serve as a starting point for a larger study on the relationships within the subfamily. The goals of this study were to confirm or disprove the monophyly of the *Pococera* complex and of the included genera. It also estimated the relationships among the genera and provided a generic synopsis and description of the new genera of the complex.

MATERIALS AND METHODS

Adult specimens (and/or photographs) were provided by the following museums and private collections: AMNH—American Museum of Natural History, New York, USA; ANIC—Australian National Insect Collection, CSIRO, Canberra, Australia;

BMNH—The Natural History Museum, London, England; CNC—Canadian National Collection, Agriculture Canada, Ottawa, Canada; CNP—Carnegie Museum, Pittsburgh, Pennsylvania, USA; CUI—Cornell University, Ithaca, New York, USA; INHS—Illinois Natural History Survey, Champaign, Illinois, USA; LACM—Los Angeles County Museum of Natural History, Los Angeles, California, USA; MNHP—Museum National d'Histoire Naturelle, Paris, France; MEM—Mississippi State Museum, Starkville, Mississippi, USA; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; TAMU—Texas A&M University, College Station, Texas, USA; TMP—Transvaal Museum, Pretoria, South Africa; UCB—Essig Museum of Entomology, University of California, Berkeley, California, USA; UMO—Hope Museum, Oxford, England; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; ZMHB—Zoologisches Museum, Humboldt Universität, Berlin, Germany; Vitor O. Becker, EMBRAPA, CPAC, Planaltina, Brazil; Daniel H. Janzen, University of Pennsylvania, Philadelphia, Pennsylvania, USA; Roy O. Kendall, San Antonio, Texas, USA; Edward C. Knudson, Bellaire, Texas, USA; Ronald H. Leuschner, Manhattan Beach, California, USA; Bryant Mather, Clinton, Mississippi, USA.

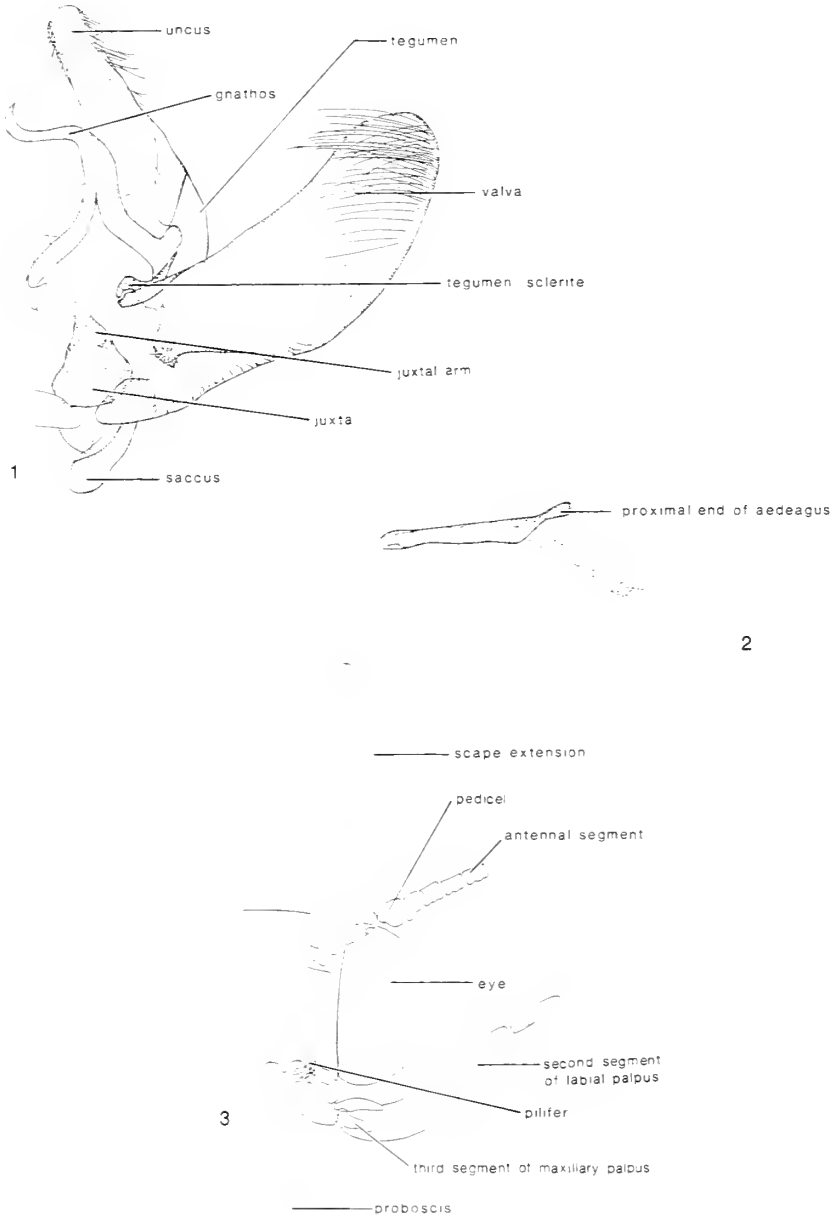
Most of the type material is located in The Natural History Museum, the National Museum of Natural History, and the Carnegie Museum. When the only known specimen of the species was the holotype, or when material was not available, a photograph of the type was used. After the *Pococera* complex was provisionally identified, 47 genera and 349 species were hypothesized to belong to the complex. The type species of each genus was dissected, and at least one male and female of approximately 82% of the species in *Pococera* complex were dissected. This figure does not represent species designated as junior synonyms and species in the checklist based on photographs of the types. Species were studied by dissection, or were included in the genus based on a photograph.

Most of this study was carried out using a Wild M5 stereoscopic dissecting microscope, but preliminary/exploratory morphological studies were carried out with a compound light microscope and a scanning electron microscope. Line drawings of representatives of each genus are provided because most of the taxa have never been illustrated. The drawings were executed using a Wild M5 stereoscopic dissecting microscope with a camera lucida attachment.

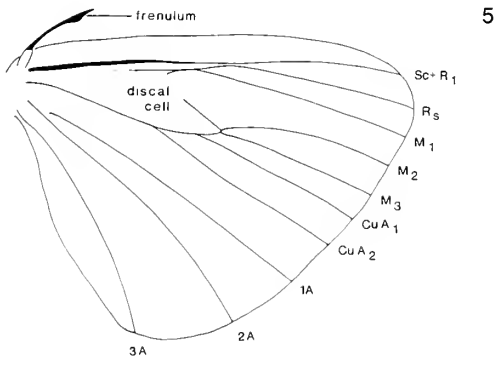
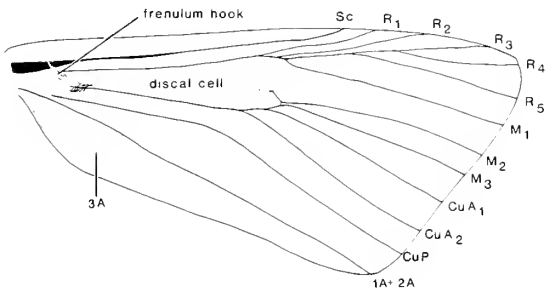
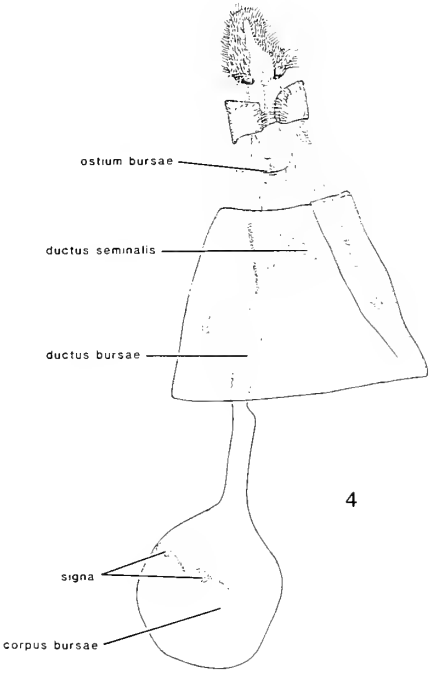
Head, legs, wings, abdomen, and genitalia of adults were dissected for this study. Heads were cleared in KOH, dissected in water, and temporarily stored in 75% alcohol. They were mounted in balsam on concavity slides, frontal side up. Wings were bleached, stained with eosin-Y and mounted in balsam. Genitalia were cleared with cold KOH and dissected in water. They were stained with chlorazol black and stored in glycerin until ready to be mounted in balsam. The genitalia were mounted on slides ventral side up. The aedeagus is small, so no attempt was made to inflate the vesica.

Terminology applied to the head (Fig. 3) and to wing veins and markings (Fig. 5) corresponds to Forbes (1923) and Wootton (1979), respectively. Terminology applied to the genitalia follows Klots (1956) and to the tympanic organs follows Maes (1985) (Figs. 1, 2, 4).

To determine the relationships of the genera of the *Pococera* complex a cladistic analysis was performed. The analysis was executed with the PHYSYS software pack-



Figs. 1-5. Terminology. 1. Male genitalia. 2. Aedeagus. 3. Male head. 4. Female genitalia. 5. Wing venation.



age written by M. Mickevich and J. S. Farris (1984). The characters were coded alphanumerically and read with the CREAD option. A description of each character and its hypothesized transformation series is discussed in the morphology section.

The DWAG.S command (with the tree buffer set to 10, the default) was used to perform a Wagner ground-plan analysis (Farris, 1970; Mickevich and Farris, 1984) that estimates relationships among taxa based on the Wagner parsimony criterion (Farris, 1983). The program uses both local and global branch-swapping. Branch-swapping searches for the most parsimonious tree by iteratively rearranging branches on an estimated tree and re-optimizing ancestral character states. Local branch-swapping rearranges terminal taxa and global branch-swapping rearranges subterminal groups. The DIAG.C command in PHYSYS calculated the consistency indices, a measure of homoplasy (Farris, 1969), for each character and tree.

MORPHOLOGY

The character numbers in the following discussion correspond to the character matrix in Table 1 and to the Summary of Characters and States.

Head. The eyes do not vary in shape or size. An ocellus, with an associated chaetosema, is always present. However, ocelli are absent in other taxa of the Pyralidae, such as the Galleriinae and occasionally the Phycitinae.

The antennae are sexually dimorphic. The antennal segments are simple in the female, but vary from laminate to serrate to bipectinate in the male. The length of the pectinations varies within genera. The antennal setae in the female always are shorter than the length of any one antennal segment. In the male, the setae vary in length along the antenna. The setae are longest near the base and on the ventral side and decrease in length toward the apex. The longest setae are usually two segments long and free, but in *Phidotricha* Ragonot they are longer than two segments and appressed to the ventral side of the antennal shaft (Fig. 43; Character 1). The pedicel is only slightly longer than the adjacent antennal segment. The scape of the female antenna is simple, not medially elongated at the base of the pedicel. The plesiomorphic condition in the male is a medial elongation of the scape that is longer than the base of the pedicel. This modification of the male scape is absent in ten genera (Fig. 31; Character 2). The length of the modification at the base of the scape and its possession of specialized setae varies within genera. The medial modification of the scape of *Milgithea* Schaus has secondary, fingerlike protrusions (Fig. 40; Character 3).

The frons is usually not sculptured, but *Mazdacis* Solis, new genus, has a lobe below the antenna extending medially to the base of the clypeus (Fig. 101; Character 4).

A proboscis is always present and fully developed, except in *Roeseliodes* Warren where it is reduced in length to about half the length of the fully developed proboscis found in the remaining Epipaschiinae (Character 5).

The pilifers vary in length within genera. A median clypeal lobe is present in all genera except *Roeseliodes* (Fig. 51; Character 6).

The labial palpus is always upturned, never porrect. The second segment of the labial palpus in the male varies in shape. Typically it is simple with no modifications (Fig. 31; Character 7), as in the female, but several modifications, interpreted as independent, occur. The genera *Quadraforma* Solis, new genus, *Mazdacis*, *Pococera* Zeller, *Tancoa* Schaus, and *Dasyvesica* Solis have a tubulate second segment of labial

palpus (fig. 22 in Solis, 1991) that surrounds specialized setae of the maxillary palpus. The second segment in *Pandoflabella* Solis, new genus is flabellate, that is, it expands to a narrow fanlike shape when water is flushed through the segment (Fig. 76). In *Macalla* Walker the distal portion of the second segment is broadened and bears a circular patch of non-deciduous setae. The position of the organ of vom Rath varies within some genera. The third segment of the labial palpus varies in length within genera.

The maxillary palpi have three segments, although studies by Hulst (1889) had suggested four segments. Scanning electron photographs of the same species studied by Hulst were examined. The disagreement results from a medial collapse of the first segment. Four and five segments are found in the more primitive groups of Lepidoptera. The base of the first segment of the maxillary palpus is typically sclerotized, but in *Mediavia* Solis, new genus, and *Deuterollyta* Lederer it is membranous and pleated (Fig. 36; Character 9). The second segment bears a proximal lobe or extension in *Anarnatula* Dyar (Fig. 9; Character 11). The place of attachment of the third segment of the maxillary palpus on the second in the male varies among genera (Character 10). The third segment adjoins the apex of the second segment (Fig. 54), the typical lepidopteran condition, in *Roeseliodes*, *Cecidipta* Berg, *Tallula* Hulst, *Phidotricha*, *Carthara* Walker, *Oneida* Hulst, *Anarnatula*, *Accinctapubes* Solis, new genus, and *Bibasilaris* Solis, new genus. In *Chloropaschia* Hampson, the third segment adjoins the second segment slightly below its apex (Fig. 31), and in *Mazdacis* and *Tancoa* it arises from the midpoint of the second segment (Fig. 58). In the remaining genera, including the outgroups *Macalla* and *Lacalma* Janse, the third segment is attached at the base of the second segment (Fig. 64). The insertion of the third segment on the second is hypothesized to transform gradually from the apical to basal position. In *Anarnatula* the midpoint of the segment of the maxillary palpus is twice as wide as the base (Fig. 9; Character 8).

Thorax. The legs are simple with no variation in tarsal spines. The number of hind tibial spurs varies in number in some genera.

The epipaschiine wing-locking device provides several characters. The frenulum consists of one bristle in the male and two bristles in the female. The bristles are tapered in all genera except *Accinctapubes*, in which they are bulbous apically in the male (Fig. 89; Character 12). There are two structures in the forewing that function to hold the frenulum, a retinaculum and a frenulum hook, both of which occur in other Pyralidae. A retinaculum, a group of small, hooked setae at the base of the wing below the Cu vein, is always present in males and females of the Epipaschiinae. In addition the frenulum hook, an extension of the Sc vein originating at the base of the wing and extending to the discocellular cell (Fig. 35; Character 13), occurs in eight genera.

Color and pattern on the wing were not used for the phylogenetic analysis because of their variability (see Solis, 1991). Many Epipaschiinae have green-tinted wings in life, but this color fades to brown or dull-yellow after they are dry. Patterns vary within some genera. The forewing of most males in *Pococera*, except *gibella* Zeller and *tertiella* Dyar, has a costal fold with a specialized tuft of scales (Fig. 127; Character 14). This feature occurs sporadically in the Phycitinae and other families in the Lepidoptera.

Wing venation has been used widely in Lepidoptera taxonomy. Fusion of wing

veins is usually considered to be derived and a full complement of veins is considered to be plesiomorphic. In the epipaschiine forewing, R_1 and R_2 may be separate or completely fused (Character 15). R_2 usually arises proximal to the discocellular cell (Character 16), but in *Mediavia* Solis, new genus it arises distal to the discocellular cell (Fig. 92). In *Macalla* and *Roeseliodes* R_3 and R_4 are fused (Fig. 50; Character 17). R_5 and M_1 are always present with M_1 forming the anterior outer corner of the discocellular cell. In the plesiomorphic condition, the cell is more than half as long as the forewing, but in *Mazdacis* and *Pococera* it is less than half the length of the forewing (Fig. 69; Character 18). M_3 and Cu_1 are fused at the base in *Lacalma* (Fig. 113; Character 19). In most genera CuA_1 and M_3 are parallel to each other, but in *Tallula* CuA_1 arches toward M_3 (Fig. 55; Character 20). The CuP vein is primitively absent in the Epipaschiinae, but re-appears in *Lacalma*, *Roeseliodes*, *Cecidipta*, *Chloropaschia*, *Quadraforma*, *Deuterollyta*, and *Accinctapubes* (Fig. 35; Character 21). $2A$ is coincident with $1A$ in most epipaschiines, but $3A$ is lost in several genera (Fig. 69; Character 22).

In the hindwing, $Sc+R_1$ and Rs may be fused at one point or separate (Fig. 35; Character 23). $Sc+R_1$ may be convexly curved, a synapomorphy of *Carthara* (Fig. 17; Character 24). Rs extends to less than half the length of the discocellular cell in most genera, but it extends farther in *Carthara*, *Tallula*, and *Cacozelia* Grote (Fig. 17; Character 25). For most epipaschiines M_2 and M_3 are separate, but fusion of M_2 and M_3 occurs in *Roeseliodes* (Fig. 50; Character 26). The amount of fusion at the base of M_2 and M_3 varies within the remaining genera. CuA_1 and CuA_2 are separate at the base. The loss of CuA_2 is a synapomorphy for *Roeseliodes* (Fig. 50; Character 27). $1A$, $2A$, and $3A$ are present in the hindwing.

Abdomen. The first eight segments that form the abdomen are simple, without any distinguishing characteristics, except for the unique sclerotized pattern on segment eight of *Chloropaschia* (Fig. 28) and *Tancoa* (Fig. 53; Character 28). The epipaschiine tympanic organs occur on the first sternum and are described and well illustrated by Minet (1983, 1985). Secondary venulae are never present in the *Pococera* complex or the entire subfamily, the Epipaschiinae (Solis and Mitter, 1992). No morphological variation was detected at the generic or specific level in the *Pococera* complex.

Male genitalia. In the epipaschiines, the tegumen articulates ventrocephalad to the vinculum, valva, and gnathos and with the uncus dorsoposteriad. The tegumen is primarily membranous and abuts only a small portion of the base of the uncus. Anteriorly, the tegumen is sclerotized at points of articulation. A synapomorphy of the Epipaschiinae is a separate "sclerite" formed by the section of the tegumen that articulates with the gnathos, which is highly sclerotized and separated by membrane from the dorsal part of the tegumen (Character 29). The term "sclerite," as used here, is not a sclerite according to Torre-Bueno (1989), because it is not part of the body wall, but it is a section of the tegumen separated by membrane. This separate sclerite does not occur in the remaining subfamilies of Pyralidae. Its distribution in the Crambidae is uncertain since this structure is usually visible only on unmounted specimens, but representatives studied did not have the sclerite. The tegumen sclerite varies in shape and length. It does not usually reach a midventral position, but in *Oneida* and *Dasyvesica* it does reach a midventral position (fig. 9 in Solis, 1991), and in *Cecidipta* it extends beyond the midventral position (Fig. 22; Character 30). The tip of the tegumen sclerite is usually pointed, that is, less broad than the base,

but in *Quadraforma*, *Phidotricha*, and *Pococera* the tip is as broad as the base (Fig. 65), and the tip is broader than the base (Fig. 22) in *Mazdacis* and *Cecidipta* (Character 31). A synapomorphy for *Tancoa* is a dorso-anterior extension of the tegumen (Fig. 59; Character 32).

One of the apomorphies for the *Pococera* complex is the presence of a saccus that is elongate, bulbous and curved up toward the anterior end of the aedeagus (Fig. 91; Character 33). The entire vinculum curves up toward the base of the aedeagus in all other epipaschiines and some other pyralids, but it does not form an evagination or saccus.

The uncus is well developed, almost as long as the vinculum in epipaschiines and is reduced only in *Roeseliodes* (Fig. 48; Character 34). The uncus has arms that are elongate ventro-anteriorly and articulate with the base of the gnathos. In some genera, the uncus has a sclerotized structure at the base (Character 35). The basal sclerotization when present is U-shaped (Fig. 19), except that in *Tallula* and *Phidotricha* it is triangular (Fig. 36; Character 63). Caudally, the uncus usually has many setae, at times extending to the middle of the uncus, but in several genera, there is only a single, distal row of setae (Fig. 65; Character 37). The width of the uncus is usually uniform, but in several genera the caudal end is wider than the width at the midpoint (Fig. 65; Character 38). Only *Tancoa* has structures that could be termed socii (Klots, 1956), arising medially from the uncus (Fig. 59; Character 39).

In the epipaschiines, the base of the gnathos articulates posteriorly with the arms of the uncus and anteriorly with the tegumen. The arms of the gnathos are always fused at the apex, and most genera have a small curve just before the apical hook. The derived condition is the absence of this curve (Fig. 28; Character 40) and occurs in *Chloropaschia*.

The valvae are usually simple; however, most genera possess a median basal lobe (Fig. 87; Character 41) that is secondarily lost in *Roeseliodes*, *Tallula*, *Phidotricha*, *Mediavia*, and *Tancoa*. The lobe is usually a short, round nub, but in *Quadraforma* it is at least twice as long as the short condition, and square (Fig. 96; Character 42). A lobe adjacent to the costa occurs in *Mediavia* and *Mazdacis* (Fig. 91; Character 43). In *Mazdacis*, the lobe extends midventrally only to the end of the costa, but in *Mediavia* it extends beyond the costa and adjoins the juxta (Fig. 91; Character 44). In *Chloropaschia*, the valva is covered with non-deciduous rows of thin setae (Fig. 28; Character 45). *Dasyvesica* has a patch of deciduous, thick setae on the sacculus (fig. 19 in Solis, 1991; Character 46). *Tancoa* has a membranous extension, covered with setae, from the apex of the valva (Fig. 59; Character 47) that does not occur elsewhere in the epipaschiines. *Lacalma* has an expanded vinculum with coremata (Fig. 111; Character 48). This condition does not appear to be present in any other epipaschiine.

In most epipaschiines the anterior end of the aedeagus, the coecum, is usually elongate and curved (Fig. 13; Character 49). A synapomorphy for *Bibasilaris* is a bilobed coecum (Fig. 84; Character 50). But in *Roeseliodes* (Fig. 49) and *Tancoa* (Fig. 60) the anterior end is short, or the coecum is absent, and the ductus ejaculatorius is found at a terminal, anterior position on the aedeagus. In the *Pococera* complex *cornuti* occur only in *Dasyvesica* (fig. 19 in Solis, 1991; Character 51) although they do occur in other genera, such as *Macalla*, outside the *Pococera* complex.

A transtilla is not present in the Epipaschiinae. The juxta in the epipaschiines

consists typically of a base with arms extending laterally and caudad around the aedeagus, but in *Macalla* the juxta is almost completely bifurcate and its arms are ventrad and caudad of the aedeagus (Fig. 107; Character 52). In most genera the arms are longer than the base of the juxta, but in *Oneida* and *Dasyvesica* the arms are as long as the base of the juxta (fig. 9 in Solis, 1991; Character 53). *Lacalma*, *Roeseliodes*, and *Cecidipta* lack arms and the juxta is entire (Fig. 22). If arms are present, they can be shorter distally than the costa of the valva (fig. 9 in Solis, 1991), or extend beyond a point perpendicular to the base of the valva (Fig. 28; Character 54). The base of the juxta may be more heavily sclerotized than the arms (fig. 19 in Solis, 1991; Character 55) as in *Dasyvesica*. The juxta can have one medial lobe or two lateral lobes anterior to the aedeagus. The base of the juxta may have a lobe that is long and pointed, extending caudally (Fig. 65), as in *Phidotricha*, *Pococera*, *Milgitha*, *Accinctapubes*, *Bibasilaris*, *Anartula* and *Toripalpus*, or that is small and round (Fig. 28) as in the remaining genera, except *Dasyvesica* and *Oneida* which lack a medial lobe. In *Dasyvesica* the base of the juxta is flat (fig. 19 in Solis, 1991), but an apomorphy for *Oneida* is a slight curve caudally of the base of the juxta (fig. 9 in Solis, 1991; Character 56). If lateral lobes are present, the lobes have round apices (Fig. 22) in *Cecidipta* and pointed apices in *Roeseliodes* (Fig. 48; Character 59).

Female genitalia. The ovipositor lobes are membranous with many, usually unmodified setae. However, *Accinctapubes* bears unique setae on the ovipositor lobes that are spatulate and distally trifurcate (Fig. 85; Character 58).

The distal margin of the lamella antevaginalis is typically membranous, but in *Macalla* it is sclerotized (Fig. 105; Character 59). A ventral membranous fold associated with the lamella antevaginalis may occur in some genera, and it may be weakly or strongly bilobed (Figs. 26, 32; Character 60). The lamella postvaginalis is typically membranous in epipaschiines, but in *Roeseliodes* it is sclerotized (Fig. 47; Character 61).

In the Epipaschiinae, the ductus seminalis originates from the ductus bursae near the ostium bursae. In the *Pococera* complex the ductus bursae is always less than half as wide as the posterior edge of the seventh segment, in contrast to a ductus that is at least half as wide as the posterior end of the seventh segment in *Macalla* and *Lacalma* (Figs. 105, 110; Character 62). The ductus bursae has no constrictions before the corpus bursae in the *Pococera* complex, but it has a constriction in *Lacalma* and *Macalla* (Figs. 105, 110; Character 63).

The corpus bursae is membranous and comprised of only one sac in the *Pococera* complex, but *Macalla* shows a derived accessory bursa (Fig. 105; Character 64). Most genera in the *Pococera* complex and *Lacalma* have a signum composed of two, separated, elongate-conical, spinelike projections on the inner surface of the bursa (Fig. 68). These are lost in *Toripalpus* (Fig. 70) and *Tallula*. *Macalla* has a signum composed of two flat, scobinate patches (Fig. 105; Character 65).

SUMMARY OF CHARACTERS AND STATES

Final character transformation series follow order in which states are listed unless otherwise specified by a character state tree using notation according to PHYSIS (Mickey and Farris, 1984).

Head. 1. Longest male antennal setae: twice as long as antennal segments and not

appressed to ventral side (0); more than twice as long as two antennal segment lengths and appressed to ventral side (1).

2. Scape extension, length: longer than base of pedicel (0); not reaching base of pedicel (1).

3. Scape extension, secondary fingerlike protrusions: absent (0); present (1).

4. Frons, lobe below antenna: absent (0); extending medially to base of clypeus (1).

5. Proboscis: fully developed (0); less than half of fully developed in length (1).

6. Clypeus, median lobe: present (0); absent (1).

7. Second segment of labial palpus: simple, with no modifications (0); concave (1); tubulate (2); flabellate (3); apex with non-deciduous setae in a circular area (4). (4-0-1-2,3).

8. Third segment of maxillary palpus, shape: midpoint almost equal in width to base (0); midpoint twice as wide as base (1).

9. First segment of maxillary palpus, base: sclerotized (0); membranous, pleated (1).

10. Third segment of maxillary palpus situated: at apex of second segment (0); slightly below apex of second segment (1); at midpoint of second segment (2); at base of second segment (3).

11. Second maxillary segment proximal lobe: absent (0); present (1).

Wing. 12. Male frenulum, apex: tapered (0); bulbous (1).

13. Frenulum hook: absent (0); present (1).

14. Forewing costal fold: absent (0); present (1).

15. Forewing R_1 and R_2 : separate (0); fused (1).

16. Forewing R_2 , origin of: distal to discocellular cell (0); proximal to discocellular cell (1).

17. Forewing R_3 and R_4 : separate (0); fused (1).

18. Discocellular cell, length: greater than half the length of the forewing (0); half forewing length or less (1).

19. Forewing M_3 and CuA_1 : separate at base (0); M_3 and CuA_1 fused at base (1).

20. Forewing CuA_1 : parallel to M_3 (0); arching toward M_3 (1).

21. Forewing CuP : absent (0); present (1).

22. Forewing 3A: not coincident with $1A + 2A$ (0); coincident with $1A + 2A$ (1).

23. Hindwing $Sc + R_1$ and Rs : fused (0); separate (1).

24. Hindwing $Sc + R_1$: straight (0); with convex curve (1).

25. Hindwing Rs , length: less than half length of discocellular cell (0); more than half length of discocellular cell (1).

26. Hindwing M_2 and M_3 : separate (0); fused (1).

27. Hindwing CuA_2 : present (0); absent (1).

Male genitalia. 28. Eighth abdominal sternum, sclerotized pattern: absent (0); present (1).

29. Tegumen, region articulating with gnathos and valvae: entire (0); a separate sclerite (1).

30. Tegumen sclerite: not reaching midventral position (0); reaching a midventral position (1); extending beyond the midventral position (2). (0-1,2)

31. Tegumen sclerite, tip: narrower than base (0); as broad as base (1); broader than base (2). (0-1,2)

32. Tegumen, dorsocaudal extension: absent (0); present (1).
33. Saccus: absent (0); present (1).
34. Uncus: almost as long as vinculum (0); half as long as vinculum (1).
35. Base of uncus, sclerotized structure: absent (0); present (1).
36. Sclerotized structure at base of uncus, shape: U-shaped (0); triangular-shaped (1).
37. Uncus setae, placement: not in a row, extending to half the length of uncus (0); a single row on caudal end of uncus (1).
38. Uncus, width at caudal end: not wider than width at midpoint (0); wider than width at midpoint (1).
39. Socii: absent (0); present (1).
40. Curve before apical hook on gnathos: present (0); absent (1).
41. Base of valva, medial lobe: absent (0); present (1).
42. Base of valva, length of medial lobe: short, round nub (0); twice as long as short condition and squareshaped (1).
43. Costa of valva, adjacent lobe: absent (0); present (1).
44. Costa of valva, length of adjacent lobe: extending midventrally to end of costa of valva (0); extending midventrally to juxta (1).
45. Valvae, non-deciduous rows of setae: absent (0); present (1).
46. Sacculus of valva, patch of thick, deciduous setae: absent (0); present (1).
47. Apex of costa of valva, membranous extension: absent (0); present (1).
48. Expanded vinculum with coremata: absent (0); present (1).
49. Ductus ejaculatorius, at anterior end of aedeagus: terminal (0); subterminal (1).
50. Anterior end of aedeagus: simple (0); bilobed (1).
51. Cornuti: present (0); absent (1).
52. Base of juxta: not bifurcate (0); completely bifurcate (1).
53. Juxta: without arms and entire (0); with arms, longer than base of juxta (1); with arms as long as base of juxta (2).
54. Juxta arms: not extending to costa of valva (0); extending beyond costa of the valva (1).
55. Juxta, sclerotization of base: equal to arms (0); more heavily sclerotized than arms (1).
56. Base of juxta, medial lobe: present, long, pointed (0); present, small, round (1); absent, flat, without convex deformation (2); absent, with convex deformation (3).
57. Juxta lateral lobes, apex: round (0); pointed (1).
Female genitalia. 58. Ovipositor lobes, setae: all simple (0); some spatulate, then terminally trifurcate (1).
59. Lamella antevaginalis, distal margin: sclerotized (0); membranous (1).
60. Lamella antevaginalis, ventral fold: absent (0); equal in width along length or weakly bilobed (1); strongly bilobed (2).
61. Lamella postvaginalis: sclerotized (0); membranous (1).
62. Ductus bursae width near ostium: at least half as wide as posterior edge of seventh segment (0); less than half as wide as posterior edge of seventh segment (1).
63. Ductus bursae constriction, posterior to ductus seminalis, constriction: absent (0); present (1).
64. Accessory bursa: absent (0); present (1).

65. Signum: absent (0); flat, scobinate patches (1); spinelike, scobinate projections (2). (1-2-0).

KEY TO GENERA OF THE *POCOCERA* COMPLEX

1. Frenulum hook present 2
- Frenulum hook absent 8
- 2(1). Scape extension in males not extending to base of pedicel 3
- Scape extension in males extending beyond base of pedicel 4
- 3(2). Postmedial line of forewing extending toward outer margin to M_2 and M_3 , then toward the base of wing to CuA_2 where it extends toward the posterior margin *Mazdacis* Solis (p. 54)
- Postmedial line of forewing curving to the base of M_2 and with white scales present extending from base to postmedial line of discal cell and between M_1 and M_2 ... *Anarnatula* Dyar (p. 15)
- 4(2). Medial line of forewing curving twice; a faint spot present on $1A + 2A$ near the margin of forewing 5
- Medial line of forewing not curving or curving once, $1A + 2A$ without spot near the margin of forewing 6
- 5(4). Postmedial line of forewing extending anterobasally from R_5 toward the costa with small patch of white scales toward the outer margin ... *Milgitha* Schaus (p. 28)
- Postmedial line of forewing extending anterodistally from R_5 toward the outer margin and toward the base behind CuA_2 , without small patch of white scales toward the outer margin *Toripalpus* Grote (p. 43)
- 6(4). Forewing without CuP , $Sc+R_1$ and Rs of hindwing separate *Accinctapubes* Solis (p. 48)
- Forewing with CuP , $Sc+R_1$ and Rs of hindwing fused 7
- 7(6). Postmedial line of forewing extending toward outer margin at M_1 and curving toward the base to posterior margin *Bibasilaris* Solis (p. 46)
- Postmedial line of forewing anterad R_5 bent abruptly toward the base *Deuterollyta* Lederer (p. 25)
- 8(1). Scape extension in males not reaching base of pedicel 9
- Scape extension in males longer than base of pedicel 12
- 9(8). Second segment of labial palpus of male not modified, a simple cylinder 10
- Second segment of labial palpus of male modified, either concave or tubular ... 11
- 10(8). Reniform spot of forewing a small dark line; medial line curving basally below reniform spot; apical area beyond postmedial line not suffused with dark scales; area between the medial and postmedial line not white *Chloropaschia* Hampson (p. 23)
- Reniform spot of forewing absent; medial line not curving basally; apical area beyond postmedial line always suffused with dark scales, area between the medial and postmedial lines nearly all white *Tallula* Hulst (p. 35)
- 11(9). Postmedial line of forewing curving toward outer margin at M_2 ; medial line not bifurcating; reniform spot absent *Phidotricha* Ragonot (p. 31)
- Postmedial line of forewing not curving toward outer margin at M_2 ; medial line bifurcating just below the reniform spot; one line extending to posterior margin and the other to base of postmedial line; reniform spot a small dark line *Quadraforma* Solis (p. 52)
- 12(8). CuP of forewing present 13
- CuP of forewing absent 14
- 13(12). Forewing length 11 mm or less, basal color gray, without white apical area or

- black spots on adterminal line *Roeseiodora* Warren (p. 33)
- Forewing length 15 mm or more, basal color beige or white, apical area white and black spots on adterminal line *Cecidipta* Berg (p. 21)
- 14(12). Sc + R₁ and Rs of hindwing fused at one point 15
- Sc + R₁ and Rs of hindwing completely separate 19
- 15(14). 3A of forewing separate from 1A + 2A 16
- 3A of forewing coincident with 1A + 2A 18
- 16(15). Second segment of labial palpus of male not modified *Oneida* Hulst (p. 30)
- Second segment of labial palpus of male modified, tubular 17
- 17(16). Postmedial line of forewing concave from M₁ to CuA₁ and then concave again to CuA₂ and posterior margin; postmedial line of hindwing absent *Dasyvesica* Solis (p. 25)
- Postmedial line of forewing extending to outer margin from M₂; postmedial line of hindwing faintly present *Pococera* Zeller (p. 39)
- 18(15). A patch of darker scales beyond postmedial line anterad of M₂; medial line bifurcating at CuA₂; lines or spots of dark scales basal to medial line of forewing absent *Pandoflabella* Solis (p. 43)
- Patch of darker scales beyond the postmedial line above M₂ absent; medial line not bifurcated; lines or spots of dark scales basal to medial line of forewing present *Tancoa* Schaus (p. 37)
- 19(14). Rs of hindwing more than half the length of discocellular cell 20
- Rs of hindwing less than half the length of discocellular cell *Mediavia* Solis (p. 50)
- 20(19). Reniform spot of hindwing extending to costa, costa never white; Sc + R₁ of hindwing straight, not curving toward costa anterad of where M₁ splits off R *Cacozelia* Grote (p. 17)
- Reniform spot of hindwing not extending to costa, costa white, Sc + R₁ of hindwing curving toward costa anterad of where M₁ splits off R *Carthara* Walker (p. 19)

TAXONOMIC SYNOPSIS

Anarnatula Dyar, 1918

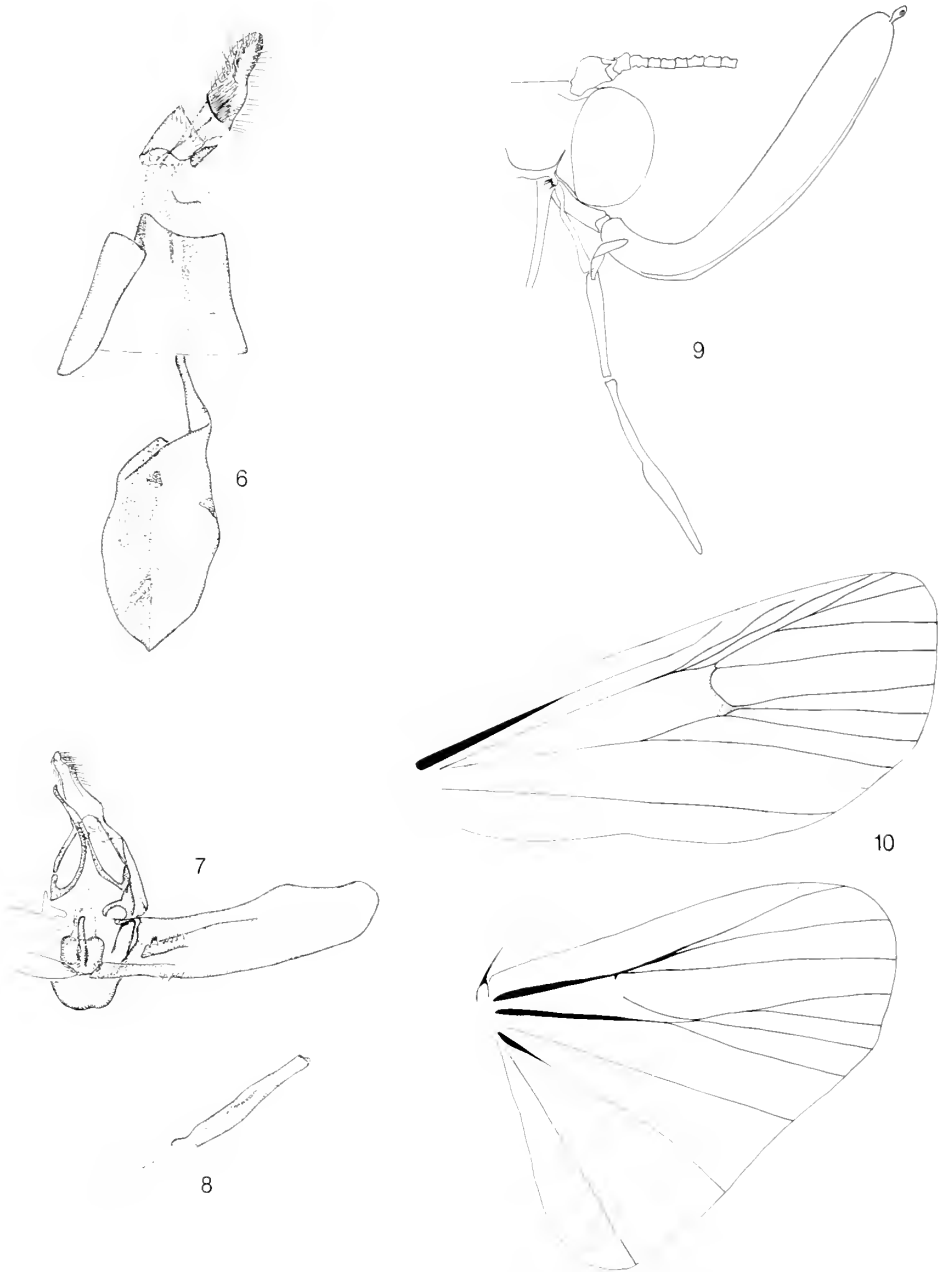
Figs. 6–10, 115

Anarnatula Dyar, 1918:371.

Diagnosis. *Anarnatula* is diagnosed by two autapomorphies on the male head (Fig. 9), a proximal lobe on the second segment of the maxillary palpus, and the third segment of the maxillary palpus with the midpoint twice as wide as the base. The presence of a frenulum hook (Fig. 10) also diagnoses this genus, but one also occurs in *Mazdacis*, *Deuterollyta*, *Bibasilaris*, *Accinctapubes*, *Milgitha*, *Toripalpus*, and the outgroup *Macalla*.

Identification synopsis. *Anarnatula* can be identified by the forewing pattern (Fig. 115) with a white postmedial line curving to the base of the wing at M₂ and white scales present from the base of the wing to the postmedial line in the discal cell and between M₁ and M₂. The hindwing has orange scales.

Anarnatula is the sister group to the *Phidotricha*-*Tallula* clade. They share the lack of an elongated scape which is also lacking in other genera. Species in all three genera are small, approximately 7 mm in wing length, in comparison to other epipaschiinae. Externally this genus can be differentiated from all other genera by the orange scales



Figs. 6–10. *Arnatula* sp. 6. Female genitalia of *A. sylea* (Druce), #201 MAS. 7. Male genitalia of *A. sylea*, #200 MAS. 8. Aedeagus of *A. sylea*, #200 MAS. 9. Male head of *A. subflavida* Dyar, #575 MAS. 10. Wings of *A. sylea*, #200 MAS.

on the hindwing. *Phidotricha* and *Tallula* are gray, brown, or white. Also a frenulum hook in the males is present in *Anarnatula*, but absent in *Phidotricha* and *Tallula*.

Type species. *Anarnatula hyporhoda* Dyar, 1918, *ibid.* 54:371, by original designation; but considered by Holland and Schaus (1925) to be a junior synonym of *Pycnulia* Druce, 1899, *Biol. Centr.-Amer., Lepid. Heter.* 2:564. Type locality. Tabasco, Mexico (*hyporhoda*) (USNM); Veracruz, Mexico (*sylea*) (BMNH).

Species examined. *subflavida* Dyar, *sylea* (Druce).

Distribution. Southern Mexico to Belem, Brazil, and the Caribbean islands of Tobago and Dominica.

Biology. No information available.

Remarks. The species included in *Anarnatula* were not changed by this study. The two species in the genus (see Nomenclatural Summary) can be distinguished by the shape of the valva in the male, size of the signa, and wing color and pattern.

Cacozelia Grote, 1877

Figs. 11–15, 116

Cacozelia Grote, 1877:263–264.

Diagnosis. *Cacozelia* is diagnosed by a unique combination of two homoplasies. 1) The Rs of the hindwing (Fig. 15) is more than half the length of the discocellular cell, which also occurs in *Carthara* and *Tallula*. 2) In the male genitalia (Fig. 12) a sclerotized structure at the base of the uncus is lacking and is a parallelism in *Roeseliodes*, *Cecidipta*, *Oneida*, *Dasyvesica*, and *Toripalpus*. The sclerotized structure is also lacking in the outgroups, *Macalla* and *Lacalma*.

Identification synopsis. *Cacozelia* can be identified by a reniform spot extended to the costa on the forewing (Fig. 116).

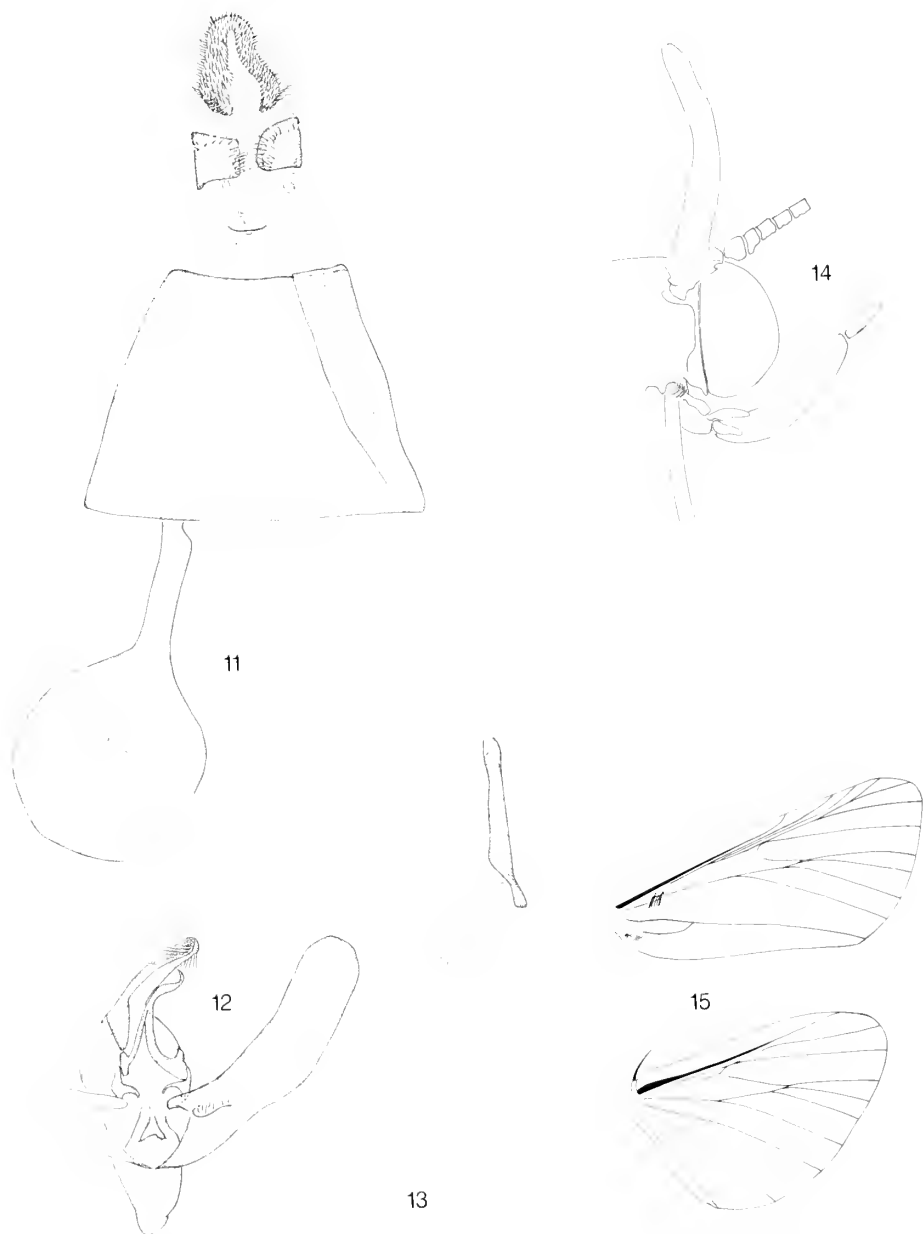
Cacozelia can be confused externally with *Toripalpus*. The species are about the same size, but *Toripalpus* lacks the extended reniform spot. Although *Toripalpus* and *Cacozelia* share a homoplasious character, the lack of the sclerotized structure at the base of the uncus, there are various other differences. *Cacozelia* lacks a frenulum hook, but *Toripalpus* has a frenulum hook. *Cacozelia* has Sc+R₁ and Rs of the hindwing completely separate, but these veins are fused at one point in *Toripalpus*. The Rs of the hindwing in *Cacozelia* is more than half the length of the discocellular cell, but is less than half the length in *Toripalpus*. The base of the juxta is present in both genera, but is small and round in *Cacozelia* and long and pointed in *Toripalpus*. In the female, *Toripalpus* lacks the ventral fold in the lamella antevaginalis, but in *Cacozelia* the ventral fold is present and equal in width or weakly bilobed. *Cacozelia* has a signum that is spinelike and scobinate, but in *Toripalpus* the signum is absent.

Type species. *Cacozelia basiochrealis* Grote, 1877, *ibid.* 19 (I):264, by monotypy. Type locality. Texas, USA (BMNH).

Species examined. *albomedialis* (Barnes & Benjamin), *basiochrealis* Grote, *elegans* (Schaus), *interruptella* (Ragonot).

Distribution. *Cacozelia basiochrealis* has been collected as far north as Kansas (USA) and *elegans* as far south as Argentina. All four species occur in southern Texas, Arizona, New Mexico and southern California.

Biology. One specimen of *elegans* from Veracruz, Mexico reared on *Mimosa pigra berlandieri* (A. Gray) (Fabaceae) is located at the USNM.



Figs. 11–15. *Cacozetia basiochrealis* Grote. 11. Female genitalia #146 MAS. 12. Male genitalia #588 MAS. 13. Aedeagus #588 MAS. 14. Male head #588 MAS. 15. Wings #588 MAS.

Remarks. *Cacozelia* was placed in synonymy with *Stericta* by Hampson (1896), but Janse (1931) could not understand Hampson's reason, and instead placed *Cacozelia* under *Jocara*. Janse also stated that he did not have access to the type species of *Jocara* and used *trabalis* Grote since it appeared to be similar. Originally, and in this work, *trabalis* was placed in *Toripalpus*. After re-definition of this genus additional species were included from a variety of other genera.

Cacozelia has four described species (see Nomenclatural Summary) distinguished by scale color and pattern. Males of the species differ in the shape of the extension of the scape, the length and shape of the third segment of the labial palpus, and the second and third segments of the maxillary palpus.

Carthara Walker, 1865

Figs. 16–20, 117

Carthara Walker, 1865:914.

Leptosphetta Butler, 1878:67. **NEW SYNONYMY.**

Pycnulia Zeller, 1881:186. **NEW SYNONYMY.**

Diagnosis. *Carthara* is diagnosed by an autapomorphy, $Sc+R_1$ of the hindwing curves toward the costa prior to the point where M_1 splits off R (Fig. 17), and a homoplasious character, R_s of the hindwing is more than half the length of the discocellular cell, which also occurs in *Cacozelia* and *Tallula*.

Identification synopsis. *Carthara* can be identified (Fig. 117) by the white costa of the forewing, and the postmedial line curving to the outer margin above Cu_2 and below Cu_2 curving toward the base of the wing.

Externally, *Carthara* can be distinguished from other genera by the prominent white costa of the forewing. *Carthara* is most similar to *Bibasilaris*. See *Bibasilaris* for a comparison of the two genera.

Type species. *Carthara albicosta* Walker, 1865, *ibid.* 33:915, by monotypy. Type locality. Amazon region (UMO). *Leptosphetta* Butler, 1878, *Trans. Ent. Soc. Lond.*: 67. Type species: *L. rabdina* Butler, by original designation. *Pycnulia* Zeller, 1881, *Horae. Soc. Ent. Ross.* 16:186. Type species: *Idia scopipes* Felder & Rogenhofer, 1875, *Reise ost. Fregate Novara (Zool.)* 2 (Abt. 2): pl. 136, fig. 39, by subsequent designation by Shibuya, 1928, *J. Fac. Agric. Kok. Imp. Univ.* 22:104.

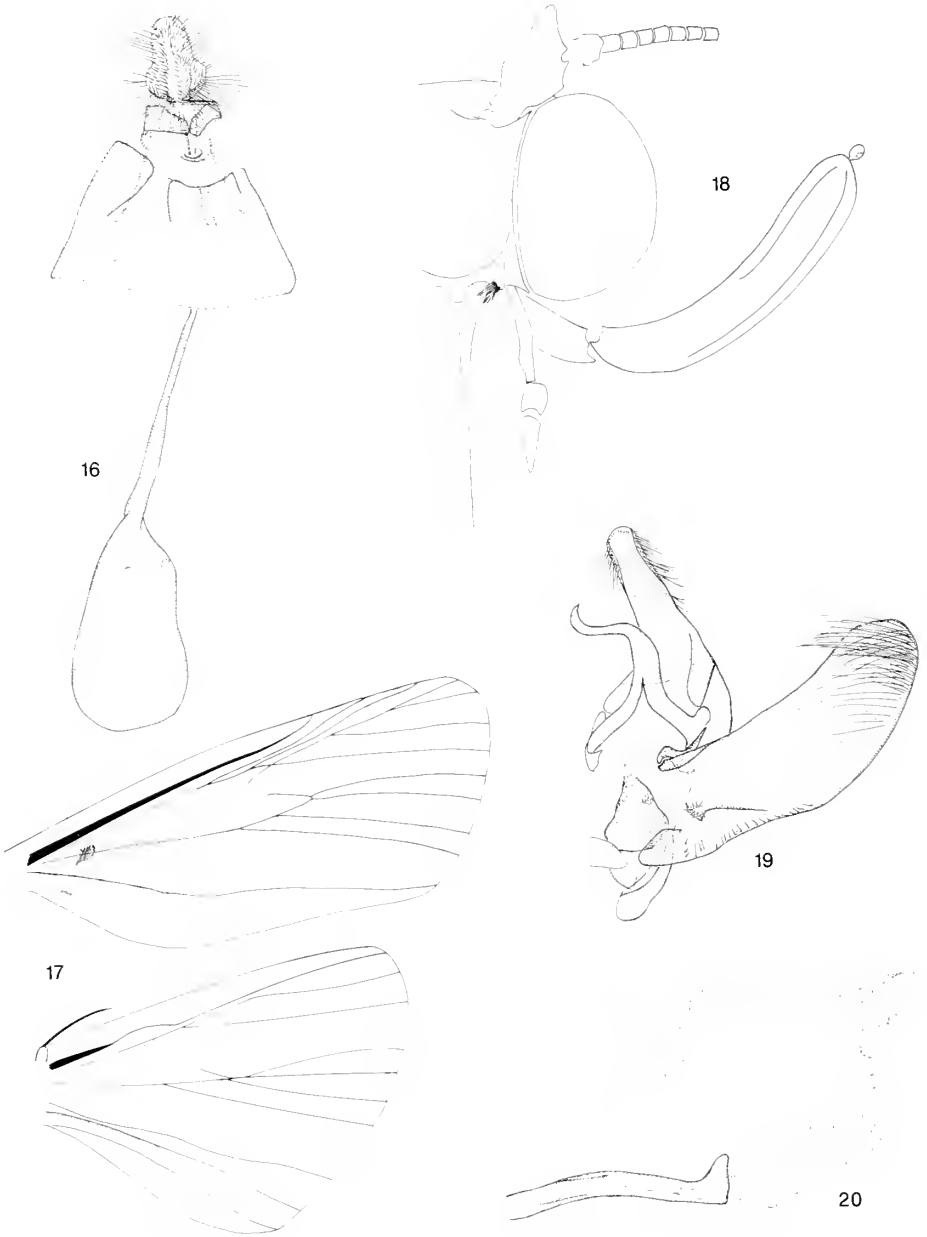
Species examined. *abrupta* (Zeller), *albicosta* (Walker).

Distribution. Southern Mexico to Brazil, with one species, *abrupta*, known from Cuba.

Biology. No information available.

Remarks. Although Hampson (1896) and Janse (1931) overlooked *Carthara albicosta* Walker, *Carthara* is the senior synonym. Hampson placed *Leptosphetta* and *Pycnulia* in *Stericta*. Hampson synonymized *ministra* and *rabdina* under *scopipes*. Janse (1931) placed *albicosta* and *scopipes* in *Leptosphetta* and outlined reasons for removing the two species from *Stericta*. He found the species to be distinct from *Stericta divitalis* (Guenée), the type species of *Stericta*, and provided a description for *Leptosphetta*. Janse pointed out that *Leptosphetta* Butler was originally placed in the Notodontidae and stated that he believed the genus to be confined to America.

Carthara is composed of two species (see Nomenclatural Summary) distinguished



Figs. 16–20. *Carthara albicosta* Walker. 16. Female genitalia #866 MAS. 17. Wings #175 MAS. 18. Male head #870 MAS. 19. Male genitalia #175 MAS. 20. Aedeagus #175 MAS.

by differences in forewing pattern and color, by the length of the scape extension in the male, and the morphology of the signa in the female.

Cecidipta Berg, 1877

Figs. 21–25, 118

Cecidipta Berg, 1877:236–238.

Acecidipta Amsel, 1956:60. **NEW SYNONYMY.**

Diagnosis. *Cecidipta* is diagnosed by an autapomorphy, a tegumen sclerite (Fig. 22) that is extended beyond the midventral line. It is also distinguished by a unique combination of the following three homoplasies: the tip of the tegumen sclerite as broad as the base, which also occurs in *Mazdacis*; an uncus with the caudal end wider than the midpoint, also occurring in *Pococera*, *Mediavia*, *Bibasilaris*, and *Lacalma*; and a single row of setae on the caudal end of the uncus, as in *Tallula*, *Phidotricha*, and *Pococera*.

Identification synopsis. The adults of *Cecidipta* are the largest in the Epipaschiinae, some females reaching 5 cm in wingspan. Average forewing length is 1.5 cm in males and 2.0 cm in females. The genus can be identified by the forewing pattern (Fig. 118) with a white apical area beyond the postmedial line, the reniform spot a thin black line from R to CuA₁, and large black spots on the adterminal line.

Cecidipta is most similar to its sister group *Roeseliodes*, but specimens of *Cecidipta* are larger than those of *Roeseliodes*. Forewings of *Roeseliodes* are usually 11 mm or less in length, and the basal color is gray. *Cecidipta* wing length is usually around 15 mm and the basal color is beige or white. The forewing of *Roeseliodes* lacks a white apical area, a reniform spot in most species, and large, black spots on the adterminal line, all of which are present in *Cecidipta*. In *Roeseliodes* the tip of the tegumen sclerite is narrower than the base, but as broad in *Cecidipta*. *Cecidipta* has an uncus that is wider at the caudal end than at the midpoint and a single row of setae on the caudal end. The caudal end of the uncus of *Roeseliodes* is less or as wide as the midpoint and lacks a single row of setae on the caudal end.

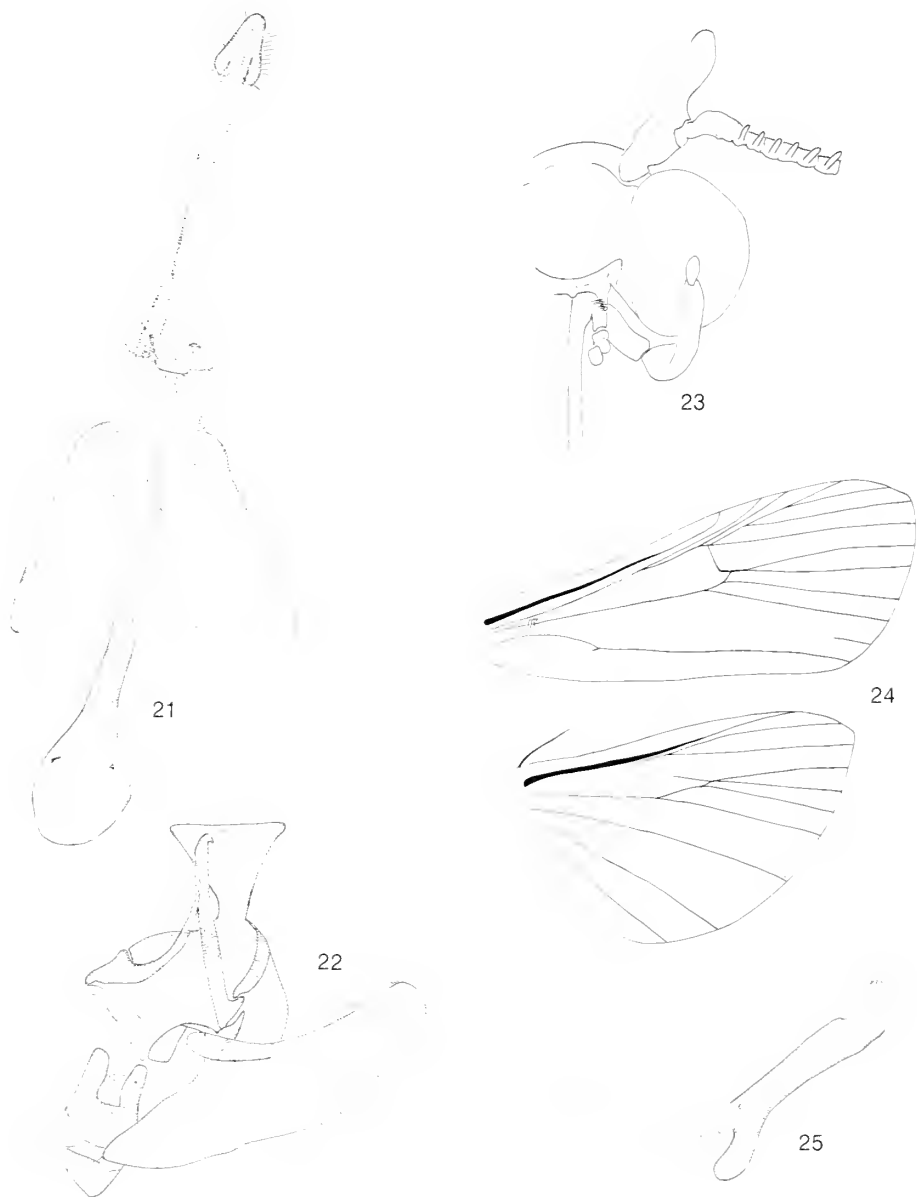
Type species. *Cecidipta excoecariae* Berg, 1877, *ibid.* 39:232–234, by monotypy. Type locality. Argentina (Buenos Aires). *Acecidipta* Amsel, 1956, *Bol. Ent. Venez.* 10:60. Type species: *A. major* Amsel, by original designation.

Species examined. *cecidiptoides* (Schaus), *excoecariae* Berg, *teffealis* (Schaus).

Distribution. Southwestern Mexico to Argentina, with one Caribbean record from Trinidad.

Biology. Berg (1877) and Bourquin (1945) described and illustrated the biology of *excoecariae* in Argentina. Berg reported that the eggs were laid in dipteran-induced galls and Bourquin reported that they were laid in cracks of the stems. According to Bourquin, the larva feeds on the foliage, but lives, eats and then pupates within stems of *Sapium haemospermum* Mueller (Euphorbiaceae). But Berg pointed out that while this method of concealment was the most common, the larva also constructs silk tubes from the galls or seeks out tubes of spiders or pupal cases of other larvae, and if these methods fail, it will web leaves together. Two specimens of *Cecidipta* sp. from Guyana reared on *Ficus* sp. ("Golden Fleece") (Moraceae) are in the USNM.

Remarks. *Cecidipta* has always been considered as distinct, but Janse (1931) discussed the inaccuracies associated with Hampson's (1896) description, particularly



Figs. 21–25. *Cecidipta excoecariae* Berg. 21. Female genitalia #634 MAS. 22. Male genitalia #635 MAS. 23. Male head #635 MAS. 24. Wings #635 MAS. 25. Aedeagus #635 MAS.

in relation to the wing venation, and attributed it to the fact that Hampson did not denude the wings. Janse provided an in-depth description of *Cecidipta*. I synonymized *Accecidipta* based on a photograph of the adult and genitalia by Amsel. More species were included from a variety of other genera.

Cecidipta has four described species (see Nomenclatural Summary). They are distinguished in the male genitalia by the width of the uncus at the apex and base, and the length of the midventral extension from the tegumen sclerite. Males also differ in the shape of the extension from the scape and the length of pectinations on the antennomeres. In females, species differences may be found in the length and width of the ductus bursae and corpus bursae, and in the dimensions of the signa.

Chloropaschia Hampson, 1906

Figs. 26–31, 119

Chloropaschia Hampson, 1906:141.

Diagnosis. *Chloropaschia* is diagnosed by two autapomorphies in the male genitalia, a valva expanded posteriorly with non-deciduous hairlike setae and a gnathos without a curve before the apical hook (Fig. 28). It is also distinguished by a combination of homoplasious characters of the head, wings and male genitalia. On the abdomen, the eighth sternum has a sclerotized pattern (Fig. 30), as in *Tancoa*. The male head (Fig. 31) has a simple second segment of the labial palpus, with no modifications, a condition which also occurs in *Bibasilaris*, *Oneida*, *Tallula*, *Roeseliodes*, *Cecidipta*, *Deuterollyta*, *Accinctapubes*, *Anarnatula*, *Cacozelia*, and *Toriipalpus*. The third segment of the maxillary palpus arises at the apex of the second segment, and this condition also occurs in *Roeseliodes*, *Cecidipta*, *Tallula*, *Phidotricha*, *Carthara*, *Oneida*, *Accinctapubes*, *Bibasilaris*, and *Anarnatula*. Sc+R₁ and Rs of the hindwing are fused (Fig. 27), as in *Pandoflabella*, *Tallula*, *Phidotricha*, *Pococera*, *Milgithea*, *Tancoa*, *Oneida*, *Dasyvesica*, *Deuterollyta*, *Bibasilaris*, *Anarnatula*, *Toriipalpus*, and *Lacalma*.

Identification synopsis. *Chloropaschia* can be identified by a forewing pattern (Fig. 119) with the reniform spot reduced to a small dark line and the medial line curved basally posterior to the reniform spot. *Chloropaschia* is most similar to its sister group, *Quadraforma*, but can also be confused with species of *Pandoflabella*. See *Quadraforma* for a comparison of the two genera.

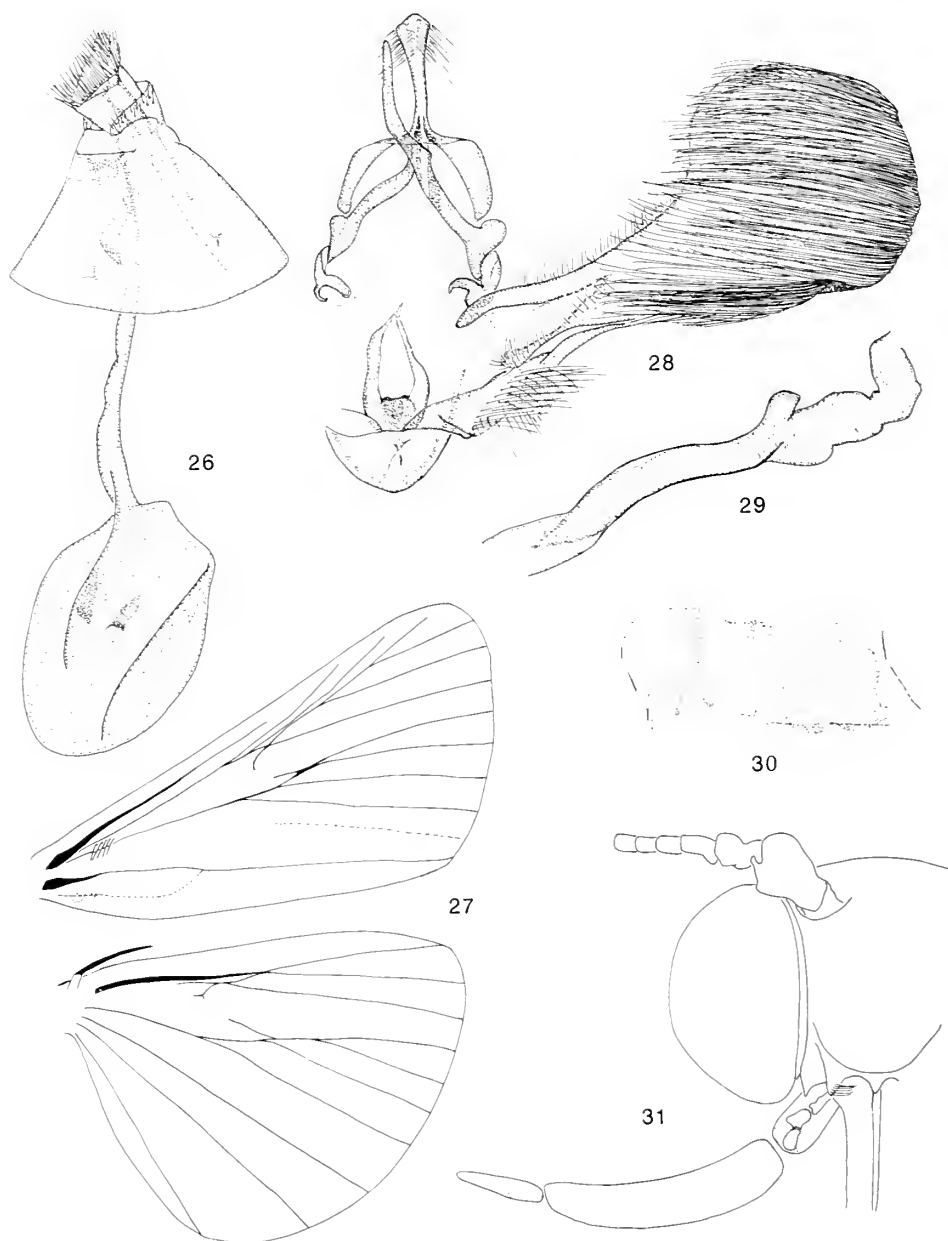
Type species. *Chloropaschia thermalis* Hampson, 1906, *ibid.* 17:141, by monotypy. Type locality. French Guiana (BMNH).

Species examined. *afflicta* (Schaus), *brithvaldia* Schaus, *contortilinealis* (Dognin), *epipodia* Schaus, *fabianalis* (Schaus), *fiachnalis* Schaus, *granitalis* (Felder & Rogenhofer), *hemileuca* Dognin, *mennusalis* Schaus, *pegalis* (Schaus), *possidia* (Schaus), *rufibasis* (Druce), *selecta* (Schaus), *thermalis* Hampson, *venantia* Schaus.

Distribution. Guatemala to northern Peru and the Amazon in Brazil.

Biology. No information available.

Remarks. Janse (1931) provided a description of *Chloropaschia* based on the type species and considered it to be a good genus. Species from a variety of other genera were included in *Chloropaschia* after the present re-definition and it now has 23 species (see Nomenclatural Summary). Species are distinguished by wing color and



Figs. 26–31. *Chloropaschia thermalis* Hampson. 26. Female genitalia #211 MAS. 27. Wings #820 MAS. 28. Male genitalia #820 MAS. 29. Aedeagus #820 MAS. 30. Eighth abdominal tergum and sternum #820 MAS. 31. Male head #820 MAS.

pattern, by the shape of the uncus and the lobe at the base of the valva, which varies in shape and length, and by the pattern of sclerotization of the eighth abdominal sternum.

Dasyvesica Solis, 1991

Fig. 135

Dasyvesica Solis, 1991:821–825.

Diagnosis. *Dasyvesica* is diagnosed by two autapomorphies in the male genitalia (fig. 19 in Solis, 1991), a patch of thick, deciduous setae on the sacculus, and the base of the juxta more heavily sclerotized than the arms. Other homoplasious synapomorphies are a tubular second segment of the labial palpus, as in *Mazdacis*, *Quadraforma*, *Cacozelia*, *Tancoa*, *Pococera*, *Milgithea* and *Lacalma*, a third segment of the maxillary palpus arising from the base of the second segment, as in *Quadraforma*, *Pandoflabella*, *Pococera*, *Milgithea*, *Mediavia*, *Cacozelia*, *Toripalpus*, *Lacalma* and *Macalla*, and cornuti present, as in the outgroup *Macalla*.

Identification synopsis. *Dasyvesica* can be identified by a forewing pattern (Fig. 135) with the postmedial line concave from M_1 to CuA_1 and then concave again to CuA_2 and the posterior margin of the wing. The reniform spot has darker scales distally. The median line is present from M_2 to $1A + 2A$.

The sister group of *Dasyvesica* is *Oneida*. See *Oneida* for a comparison of the two genera.

Type species. *Pococera nepomuca* Schaus, 1925, Ann. Carn. Mus. 16:16. Type locality. Santa Cruz de la Sierra, Bolivia (CNP).

Species examined. *nepomuca* (Schaus), *lophotalis* (Hampson), *crinitalis* (Schaus).

Distribution. Venezuela and Bolivia to Quintana Roo in Mexico and to Jamaica in the Caribbean.

Biology. No information available.

Remarks. The three species in *Dasyvesica* were previously placed in *Jocara* and *Pococera*.

Dasyvesica was recently described (Solis, 1991) with three included species (see Nomenclatural Summary), and specimens of least two new species from South America are in the USNM. Species are distinguished by wing color and pattern, the area in the sacculus that is covered by setae, and the length of the extension of the scape.

Etymology. This generic name is derived from the Greek *dasys* meaning “thick with hair” and the Latin *vesica* (feminine) meaning “bladder” in reference to the cornuti on the vesica.

Deuterollyta Lederer, 1863

Figs. 32–36, 120

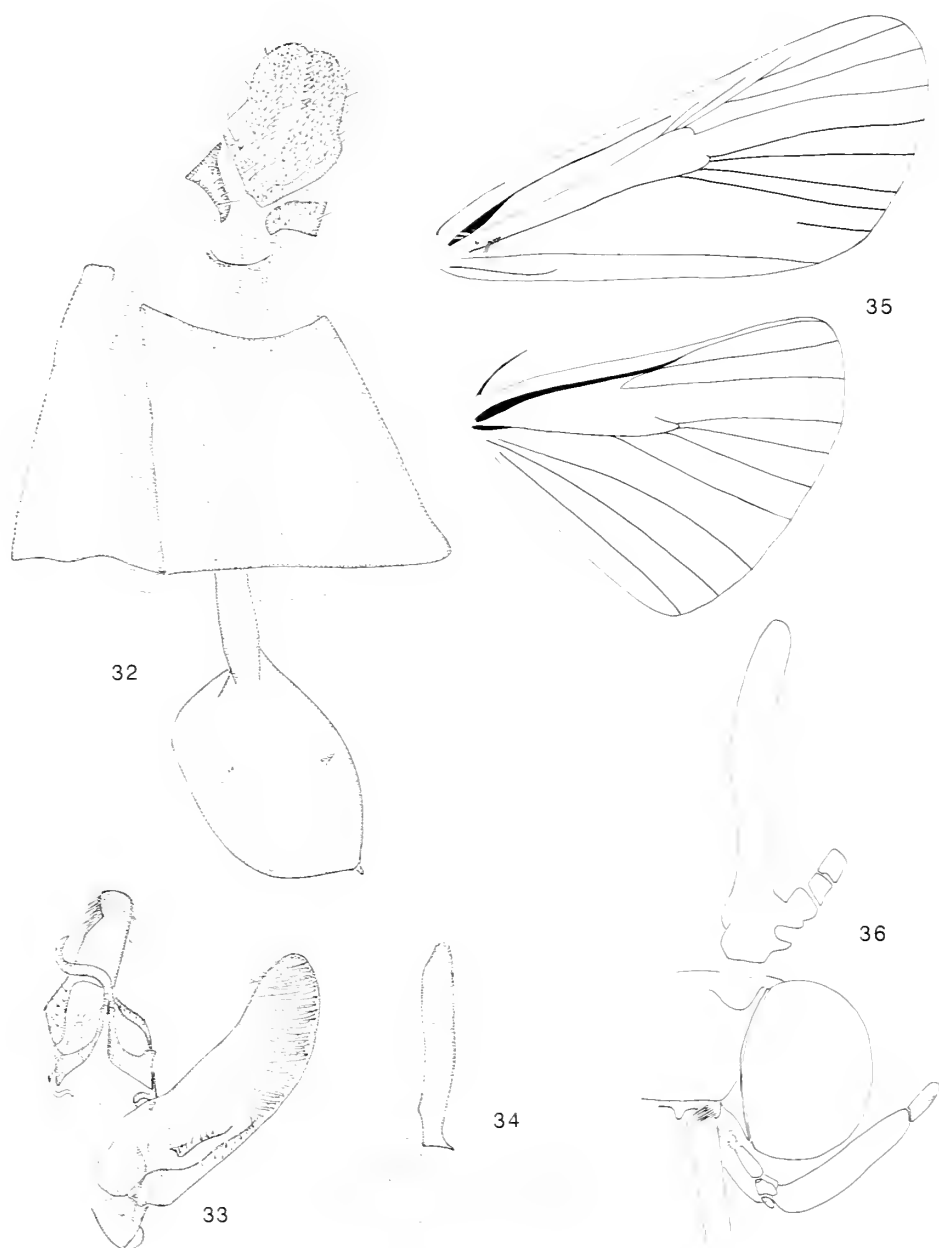
Deuterollyta Lederer, 1863:358–359.

Winona Hulst, 1888:113. **NEW SYNONYMY.**

Oedomia Dognin, 1906:120. **NEW SYNONYMY.**

Ajocara Schaus, 1925:15. **NEW SYNONYMY.**

Ajacania Schaus, 1925:14. **NEW SYNONYMY.**



Figs. 32–36. *Deuteroltya conspicualis* Lederer. 32. Female genitalia #889 MAS. 33. Male genitalia #888 MAS. 34. Aedeagus #888 MAS. 35. Wings #389 MAS. 36. Male head #389 MAS.

Diagnosis. *Deuterollyta* is diagnosed by a unique combination of three homoplasious wing characters; CuP present in the forewing, also occurring in *Roeseliodes*, *Cecidia*, *Chloropaschia*, *Quadraforma*, *Bibasilaris*, and *Lacalma*; frenulum hook present, as in *Mazdacis*, *Milgitha*, *Accinctapubes*, *Bibasilaris*, *Toripalpus* and *Macalla*; and Sc+R₁ and R₅ in the hindwing fused, as in *Chloropaschia*, *Pandoflabella*, *Tallula*, *Phidotricha*, *Pococera*, *Milgitha*, *Tancoa*, *Oneida*, *Dasyvesica*, *Bibasilaris*, *Anarnatula*, *Toripalpus* and *Lacalma*.

Identification synopsis. *Deuterollyta* can be identified by a forewing pattern (Fig. 120) with the postmedial line above R₅ shifting abruptly toward the base of the wing. *Deuterollyta* is most closely related to *Mediavia*. See *Mediavia* for a comparison of the two genera.

Type species. *Deuterollyta conspicualis* Lederer, 1863, *ibid.* 7 (10):359, Taf. 7, Figs. 16, 17. Lectotype designated Munroe (1958), p. 510. Type locality. Brazil (BMNH). *Winona* Hulst, 1888, *Ent. Am.* 4:113. Type species: *Toripalpus incrustalis* Hulst by original designation. *Oedomia* Dognin, 1906, *ibid.* 50:120. Type species: *O. hispida* Dognin by original designation. *Ajocara* Schaus, 1925, *ibid.* 16:15. Type species: *A. amazona* Schaus by original designation. *Ajacania* Schaus, 1925, *ibid.* 16:14. Type species: *A. steinbachalis* Schaus by original designation.

Species examined. *abachuma* (Schaus), *aidana* (Schaus), *albiferalis* (Hampson), *albimedialis* (Hampson), *amazonalis* (Schaus), *anastasia* (Schaus), *ansberti* (Schaus), *basilata* (Schaus), *cantianilla* (Schaus), *chlorisalis* (Schaus), *claudalis* (Moeschler), *cononalis* (Schaus), *conrana* (Schaus), *conspicualis* Lederer, *cristalis* Felder & Rogenhöfer, *dapha* (Druce), *francesca* Jones, *fuscifusalis* (Hampson), *hispida* (Dognin), *majuscula* Herrich-Schaeffer, *maroa* (Schaus), *multicolor* (Dognin), *nigripuncta* (Schaus), *oediperalis* (Hampson), *prudentia* (Schaus), *pyropicta* (Schaus), *ragonoti* Moeschler, *raymonda* (Schaus), *subcurvalis* (Schaus), *subfusca* (Schaus), *suiferens* (Dyar), *tenebrosa* (Schaus), *translinea* (Schaus), *umbrosalis* (Schaus), *yva* (Schaus), *zetila* (Druce).

Distribution. Florida and Mexico to Brazil and Argentina.

Biology. Specimens with the following host-plant data are in the USNM: *aidana* from Cuba on *Picramnia pentandra* Sw. (Simaroubaceae); *chlorisalis* on avocado (Lauraceae) from Costa Rica; *majuscula* on avocado from Honduras and Florida; *zetila* on avocado from Peru; *subcurvalis* on avocado from Honduras, Costa Rica and Venezuela. Upon describing *perseella*, Barnes and McDunnough also noted that one specimen was reared from *Persea americana* Mill. (cited as *P. gratissima* by the authors) (Lauraceae). Martorell (1976) listed the following leafwebbers from Puerto Rico on representatives of Lauraceae: *majuscula*, collected at Cayey, 1,800 ft on *Nectandra sintensii* Mez (Lauraceae); at Cayey and Arecibo on *Ocotea leucoxylon* (Sw.) Gómez Maza (Lauraceae); and at Cayey, 1,500 ft on *Phoebe elongata* (Vahl) Nees (Lauraceae); and *ragonoti* at El Pastillo and Mona Island on *Conocarpus erectus* L. (Combretaceae).

Remarks. Hampson (1896) treated *Deuterollyta* as a junior synonym under *Stericta*, but Janse (1931) disagreed with Hampson's placement based on wing venation and placed it in *Jocara*. Janse did not know whether *Deuterollyta* was "worth preserving" as he could not find any differences between it and *Jocara trabalis* Grote. Holland and Schaus (1925) treated *Deuterollyta* as a junior synonym of *Jocara*. I have resurrected *Deuterollyta* based on the synapomorphies listed in the diagnosis. Therefore,

many species described in *Jocara* are now placed in this genus. The true identity of *Jocara* is not known. The type species, *Jocara fragilis* Walker, was described from one female from the Dominican Republic. Only one other specimen, another female, from Haiti was located.

Deuterollyta has 36 species (see Nomenclatural Summary). I suspect that some will prove to be species complexes. Species are distinguished by scale color and pattern. They are also recognized by modifications of the extension of the scape, the uncus and by the dimensions of the signa.

Milgithea Schaus, 1922

Figs. 37–41, 121

Milgithea Schaus, 1922:208.

Diagnosis. *Milgithea* is diagnosed by one autapomorphy, the secondary fingerlike protusions on the scape extension (Fig. 40).

Identification synopsis. *Milgithea* can be identified by a forewing pattern (Fig. 121) having a prominent reniform spot sometimes extending toward the costa, a postmedial line extending from R_5 basally with a small patch of white scales toward the outer margin, and a medial line twice curved. The hindwing has a spot on 1A near the margin.

Milgithea and *Toripalpus* are very similar in that they both have a medial line in the forewing that is twice curved and a faint spot on 1A near the margin of the hindwing, but they are externally distinguishable. In *Milgithea* the postmedial line has a small patch of white scales toward the outer margin and extends from R_5 toward the costa basally, but in *Toripalpus* the postmedial line extends from R_5 toward the outer margin and toward the base of the wing after CuA_2 . Both *Milgithea* and *Toripalpus* have an elongated scape, but the scape extension of *Milgithea* has secondary fingerlike projections. The second segment of the labial palpus of the *Milgithea* is tubular, and in *Toripalpus* it is simple with no modifications. *Milgithea* has a U-shaped sclerotized structure at the base of the uncus that is absent in *Toripalpus*. The signa of *Milgithea* are two spinelike, scobinate projections, whereas the signa are absent in *Toripalpus*.

Type species. *Pococera melanoleuca* Hampson, 1896, Trans. Ent. Soc. Lond. Part IV: 458, by original designation. Type locality. Colombia (BMNH).

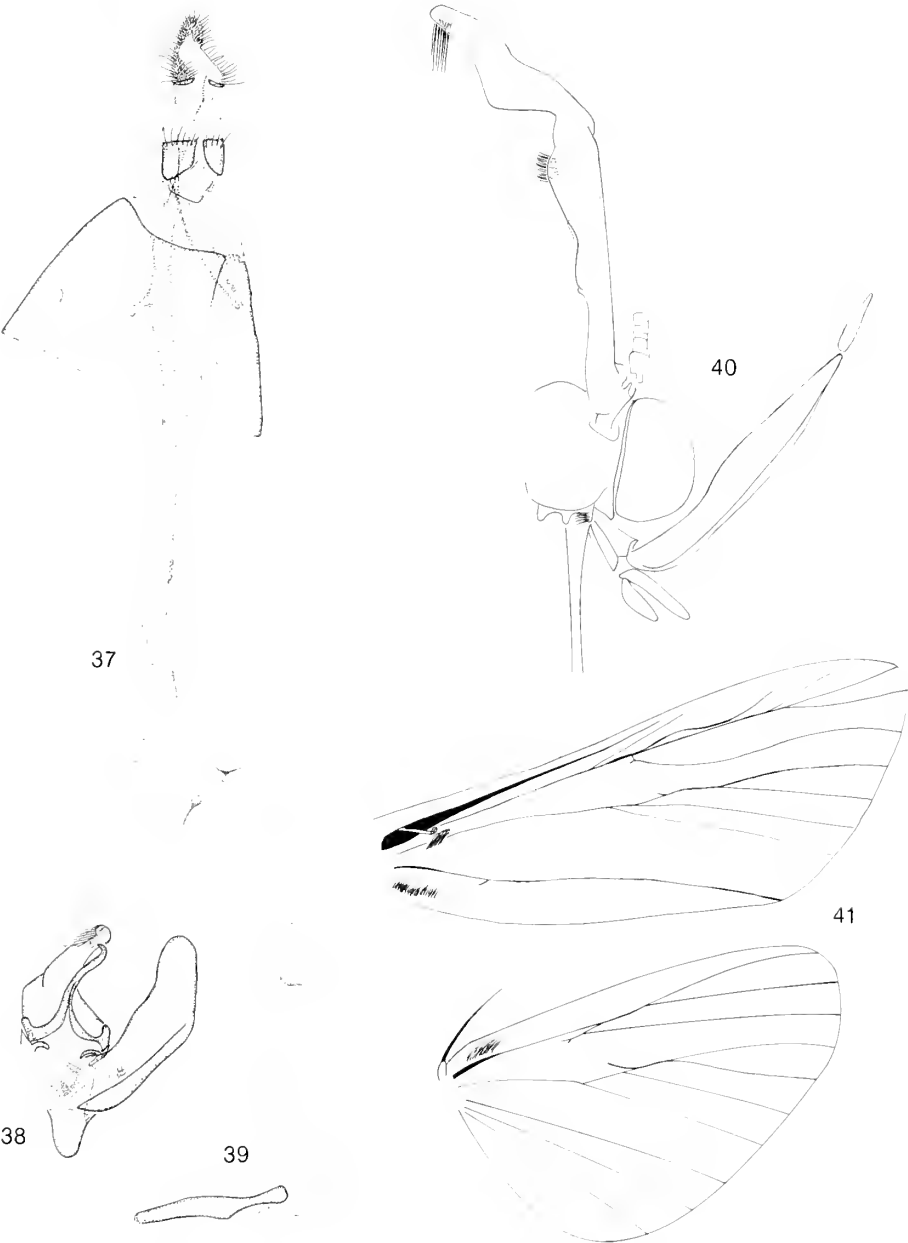
Species examined. *alboplagialis* (Dyar), *melanoleuca* (Hampson), *rufiapicalis* (Hampson), *suramisa* (Schaus), *trilinearis* (Hampson).

Distribution. Mexico and Florida south to Brazil; the only species in the Caribbean is *trilinearis*.

Biology. Adults of *trilinearis* in the USNM have labels that state they were reared from larvae on *Manilkara emarginata* Britton & P. Wilson (Sapotaceae) from Middle Torch Key and Sugarloaf Key, Florida.

Remarks. Janse (1931) provided a description and stated that *Milgithea* was close to *Jocara* (based on *trabalis* Grote) when he studied the genitalia. That *Toripalpus trabalis* is closely related to *Milgithea* is substantiated by this study.

Milgithea has five species (see Nomenclatural Summary), three added after redefinition of the genus. They are extremely diverse, but can be identified by wing



Figs. 37–41. *Milgitheia melanoleuca* (Hampson). 37. Female genitalia #184 MAS. 38. Male genitalia #226 MAS. 39. Aedeagus #226 MAS. 40. Male head #226 MAS. 41. Wings #183 MAS.

color and pattern. The extension of the scape and maxillary and labial palpi in the male are highly modified and variable.

Oneida Hulst, 1889

Fig. 122

Oneida Hulst, 1889:63.

Diagnosis. *Oneida* has one autapomorphy, the base of the juxta lacks a medial lobe, but with a convex midventral deformation (fig. 9 in Solis, 1991); and one homoplasious character, the second segment of the labial palpus is simple, with no modifications (fig. 9 in Solis, 1991), also occurring in *Bibasilaris*, *Tallula*, *Chloropaschia*, *Roeseliodes*, *Cecidipta*, *Deuterollyta*, *Accinctapubes*, *Anarnatula*, *Cacozelia*, and *Toripalpus*.

Identification synopsis. *Oneida* can be identified by a forewing pattern (Fig. 122) with the postmedial line concave proximally only to M_2 , and prominent black scales proximally to the postmedial line.

The sister group of *Oneida* is *Dasyvesica*. *Oneida* has a postmedial line concave proximally only from the costa to M_2 and in *Dasyvesica* it is concave from the costa to M_1 and then again at CuA_1 to the posterior margin of the wing. *Oneida* has prominent black scales proximal to the postmedial line from the costa to M_2 and *Dasyvesica* has dark scales proximally to the median line from M_2 to $1A + 2A$. The medial line is not present in *Oneida*. *Oneida* is diagnosed by a juxta which lacks a medial lobe with a slight convex midventral deformation, whereas *Dasyvesica* also lacks a medial lobe, but midventrally it is flat. *Oneida* has a second segment of the labial palpus that is simple, but in *Dasyvesica* it is tubular. In *Oneida* the third segment of the maxillary palpus arises at the apex of the second segment, and in *Dasyvesica* it arises at the base of the second segment.

Type species. *Oneida lunulalis* Hulst, 1889, *ibid.* 5(3): 64, by monotypy. Type locality: Canada, New York (AMNH).

Species examined. *lunulalis* Hulst, *luniferella* Hulst, *marmorata* (Schaus), *mejona* Schaus, *grisiella* Solis.

Distribution. Eastern North America from Canada to Florida, west to Colorado, and south to Costa Rica.

Biology. One specimen has been reared on red oak in mid-August in southern Ontario (Prentice et al., 1965), one specimen on beech in September in Grenville (Raizenne, 1952), and one specimen on *Quercus* sp. (Solis, 1991), later found to have fed on both red and white oak (T. Harrison, pers. comm.). Specimens have been caught at elevations of up to 7,900 ft.

Remarks. Hampson (1896) placed *Oneida* under *Tioga*. Janse (1931) resurrected the genus based on venation. Based on labial and maxillary palpi he believed that *Oneida* was closely related to *atrifascialis* Hulst and *aplastella* Hulst, but this study does not support his hypothesis. The species *atrifascialis* is placed in *Tallula* and *aplastella* in *Pococera*.

The species *grisiella* was added to this genus after re-definition. *Oneida* was recently revised (Solis, 1991). Species are distinguished by wing color and pattern. They are also defined by dimensions of male genitalic components and the ratio of signum length to diameter of its base in the female.

Phidotricha Ragonot, 1888

Figs. 42–46, 123

Phidotricha Ragonot, 1888:139.*Eutrichocera* Hampson, 1904:182. **NEW SYNONYMY.***Jocarula* Dyar, 1925:219. **NEW SYNONYMY.**

Diagnosis. *Phidotricha* is diagnosed by one unique autapomorphy, the hairlike setae on the antennae long and appressed on ventral side, and by one homoplasy, the tip of the tegumen sclerite as broad as the base (Fig. 44), as in *Quadraforma* and *Pococera*.

Identification synopsis. *Phidotricha* can be identified by a forewing pattern (Fig. 123) with the postmedial line curving toward the outer margin at M_2 and a median line with dark scales from M_2 to the posterior margin.

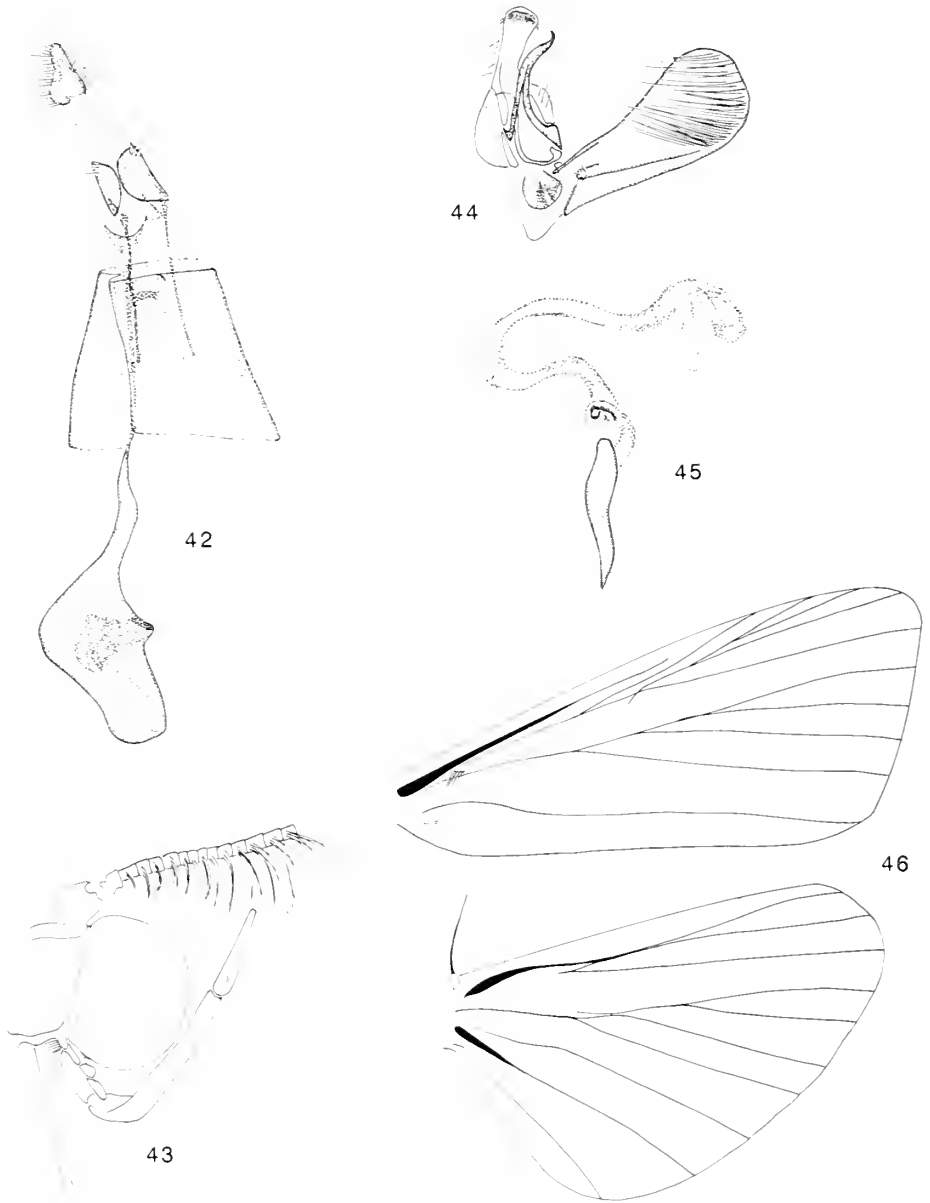
Phidotricha is the sister group of *Tallula*. Based on wing pattern, it is difficult to confuse the two, but *Phidotricha* can be confused with some species of *Pococera*. The males of *Phidotricha* have the very long hairlike setae on the antenna that are lacking in *Pococera* males. Males and females of *Phidotricha* can be distinguished by a median line in the forewing with dark scales from M_2 to the posterior margin that does not occur in *Pococera*. *Phidotricha* and *Pococera* share many homoplasies, but *Phidotricha* has a scape that is not elongated, and is elongated in *Pococera*. The second segment of the labial palpus is concave in *Phidotricha* and tubular in *Pococera*. The third segment of the maxillary palpus is at the apex of the second segment in *Phidotricha* but at the base of the second segment in *Pococera*. In the forewing R_1 and R_2 are separate in *Phidotricha*, but fused in *Pococera*. R_3 and R_4 of the forewing in *Phidotricha* are fused, but separate in *Pococera*. The discocellular cell in *Phidotricha* is half or less the forewing length, and in *Pococera* it is greater than half the length. In *Phidotricha* the sclerotized structure at the base of the uncus is triangular-shaped, but it is U-shaped in *Pococera*. The width of the uncus at the caudal end is not wider than the width at the midpoint in *Phidotricha*, but it is wider than the midpoint in *Pococera*. The medial lobe at the base of the valva is absent in *Phidotricha* and present in *Pococera*.

Type species. *Phidotricha erigens* Ragonot, 1888, *ibid.* 6(8): 139, by monotypy. Type locality. Puerto Rico (MNHP). *Eutrichocera* Hampson, 1904, *ibid.* 14 (81): 182. Type species: *E. paurolepidalis* Hampson by monotypy. *Jocarula* Dyar, 1925, *ibid.* 13: 219. Type species: *J. agriperda* Dyar by monotypy.

Species examined. *agriperda* (Dyar), *erigens* Ragonot, *insularella* (Ragonot), *limalis* (Schaus), *sadotha* (Schaus), *vedastella* (Schaus).

Distribution. Southern Florida and northern Mexico to Brazil. Common in the Caribbean.

Biology. Specimens have been reared on major agricultural crops such as corn, sorghum, lima beans and tropical fruit plants such as tamarind and loquat. The biology of *erigens* Ragonot, which in the economic literature has been misidentified as *atramentalis* Lederer, was described by Hoyle (1961), and the larval and pupal stages described by Passoa (1985). Martorell (1976) listed *atramentalis* on *Clerodendrum squamatum* Vahl (Verbenaceae), *Mangifera indica* L. (Anacardiaceae) and buds of *Terminalia catappa* L. (Combretaceae); and *insularella* in "bulbs" of *Agave sisalana* Perrine (Amaryllidaceae).



Figs. 42–46. *Phidotricha erigens* Ragonot. 42. Female genitalia #846 MAS. 43. Male head #845 MAS. 44. Male genitalia #845 MAS. 45. Aedeagus #845 MAS. 46. Wings #521 MAS.

Remarks. Hampson (1896) synonymized *Phidotricha erigens* under *Pococera atramentalis* based on the lack of an extension from the scape. Janse (1931) found it "peculiar" that certain aspects to the genitalia of *atramentalis* and *gibella*, the type of *Pococera*, were so different. I resurrected *Phidotricha* when the types of *erigens* Ragonot and *atramentalis* Lederer were studied and found not to be conspecific or congeneric. In this study *atramentalis* is placed in *Tallula*. Holland and Schaus (1925) synonymized the two species and placed them in *Pococera* as did Hampson (1896).

Phidotricha has seven species names (see Nomenclatural Summary) although it is not clear how many biological species are involved. Delineation of species may prove to be difficult because genitalia and head structures appear similar, varying only in size. Species are recognized by wing color and pattern.

Roeseliodes Warren, 1891

Figs. 47–51, 124

Roeseliodes Warren, 1891:435.

Diagnosis. *Roeseliodes* has many autapomorphies: a reduced proboscis, a clypeus with median lobe absent (Fig. 51), hindwing with CuA_2 lacking and M_2 and M_3 fused (Fig. 50), an uncus half as long as vinculum, a juxta with two lateral lobes and pointed at the apex (Fig. 48), and a sclerotized lamella postvaginalis (Fig. 47). The following homoplasious characters also are diagnostic of this genus: a second segment of the labial palpus simple, with no modifications, also occurring in *Bibasilaris*, *Oneida*, *Tallula*, *Chloropaschia*, *Cecidipta*, *Deuterollyta*, *Accinctapubes*, *Anarnatula*, *Cacozeilia*, and *Toripalpus*; the forewing R_3 and R_4 fused, as in *Macalla*; a third anal vein not coincident with the second anal vein, also occurring in *Tallula*, *Phidotricha* and *Tetralopha*, *Oneida*, *Dasyvesica*, and *Anarnatula*; a medial lobe absent at the base of the valva, as in *Tallula*, *Phidotricha*, *Mediavia*, and *Tancoa* and in the outgroup *Macalla*; and the ductus ejaculatorius terminal, which also occurs in *Tancoa*.

Identification synopsis. *Roeseliodes* can be identified by the forewing pattern (Fig. 124) with a black, prominent medial line curving out medially.

Roeseliodes is very distinct based on its many autapomorphies. It is most similar to *Cecidipta*. See *Cecidipta* for a comparison with *Roeseliodes*.

Type species. *Roeseliodes ochreosticta* Warren, 1891, *ibid.* 7:435, by original designation. Type locality. Rio de Janeiro, Brazil (BMNH).

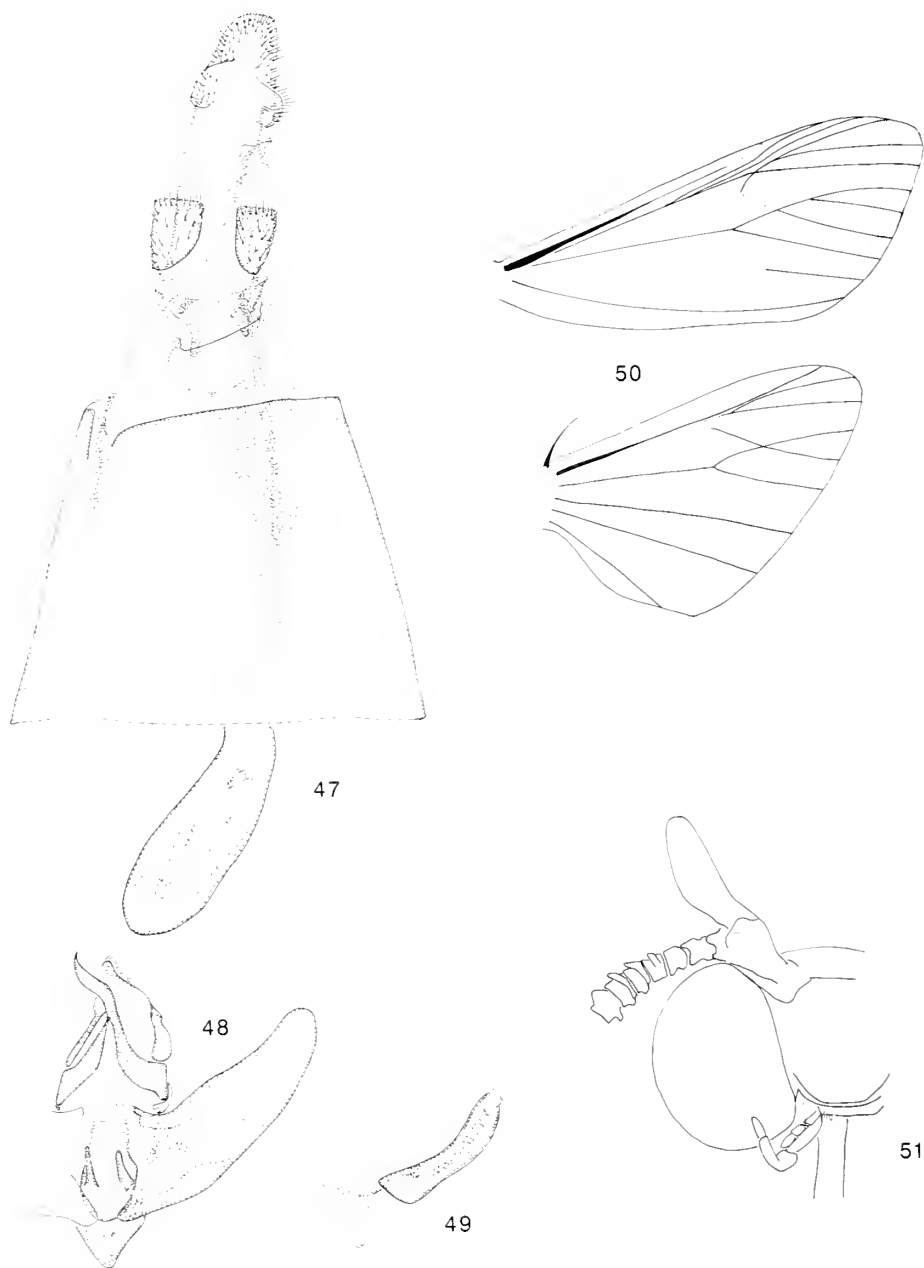
Species examined. *celsusalis* (Schaus), *goanta* (Schaus), *goantoides* (Amsel), *ochreosticta* Warren, *petamona* (Schaus), *pontealis* (Schaus).

Distribution. Costa Rica to southern Brazil.

Biology. No information available.

Remarks. Hampson (1896) synonymized *Roeseliodes* under *Stericta*, and Holland and Schaus (1925) later resurrected the genus.

Species from a variety of other genera were included in this genus after re-definition, and it now includes six species (see Nomenclatural Summary) that differ in wing color and pattern. There are also differences in the shape of the uncus and length of the extension of the scape in males, the amount of sclerotization in the lamella postvaginalis, the size of the corpus bursae, and length of the ductus bursa and signa.



Figs. 47-51. *Roeseliodes ochreosticta* Warren. 47. Female genitalia #490 MAS. 48. Male genitalia #491 MAS. 49. Aedeagus #491 MAS. 50. Wings #491 MAS. 51. Male head #491 MAS.

Tallula Hulst, 1888

Figs. 52–56, 125

Tallula Hulst, 1888:115.

Diagnosis. *Tallula* is diagnosed by one autapomorphy, vein CuA_1 of the forewing arches toward M_3 (Fig. 55), and several homoplasious characters, a simple second segment of the labial palpus, with no modifications (Fig. 54), also occurring in *Bibasilaris*, *Oneida*, *Chloropaschia*, *Roeseliodes*, *Cecidipta*, *Deuterollyta*, *Accinctapubes*, *Cacozelia*, and *Toripalpus*; Rs of the hindwing more than half the length of discocellular cell, as in *Carthara* and *Cacozelia*; the medial lobe at the base of the juxta small and round, as in *Chloropaschia*, *Quadraforma*, *Pandoslabella*, *Mazdacis*, *Carthara*, *Mediavia*, *Tancoa*, *Deuterollyta*, and *Cacozelia*; and the corpus bursae lacks a signa as in *Toripalpus*.

Identification synopsis. *Tallula* can be identified by a forewing pattern (Fig. 125) consisting of an apical area beyond the postmedial line that is always suffused with dark scales, an area between the medial and postmedial line that is almost all white, and an area between the basal and medial line with dark scales.

Tallula is the sister group of *Phidotricha*, but as mentioned previously they are not easily confused. *Phidotricha* has gray or brown scales on the entire forewing. *Tallula* has dark scales, usually brown, apically and between the basal and medial line of the forewing, and white scales that form the basal field, especially between the medial and postmedial line. On the male antennae *Phidotricha* has setae that are more than two antennal segments long, whereas in *Tallula* they are only twice as long as two antennal segments. The second segment of the labial palpus is concave in *Phidotricha*, and in *Tallula* it is simple with no modifications. The origin of R_2 in the forewing of *Phidotricha* is distal to the discocellular cell, but in *Tallula* the origin is proximal to the cell. R_3 and R_4 of the forewing are fused in *Phidotricha*, but separate in *Tallula*. In the hindwing Rs is less than half the length of the discocellular cell in *Phidotricha*, but more than half the length of the cell in *Tallula*. The tip of the tegumen sclerite in *Phidotricha* is as broad as the base, and in *Tallula* it is less broad than the base. In *Phidotricha* the medial lobe at the base of the juxta is long and pointed, but small and round in *Tallula*. *Phidotricha* has two spinelike signa, but *Tallula* lacks the signa.

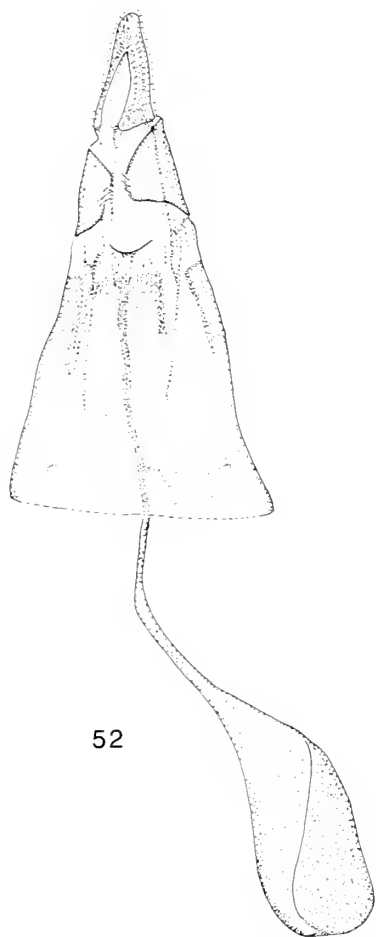
Type species. *Tetralopha atrifascialis* Hulst, 1886, Trans. Am. Ent. Soc. 13: 160, by subsequent designation. Type locality. Texas, USA (AMNH).

Species examined. *atrifascialis* (Hulst), *beroella* (Schaus), *fieldi* Barnes & McDunnough, *melazonalis* Hampson, *watsoni* Barnes & McDunnough.

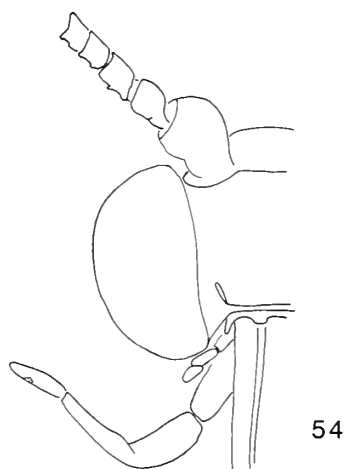
Distribution. In North America species occur from North Carolina to Arizona, Texas, southern California south to Mexico. They are also present throughout Central America to Panama and in the Caribbean. In South America, species occur in Venezuela, Bolivia, French Guiana and the Amazon Basin of Brazil.

Biology. Kimball (1965) reported that larvae had been reared on Rutaceae (lemon, orange, grapefruit) in Florida. Members of this genus have been reared on live oak in Mississippi according to specimens in the USNM.

Remarks. Hampson (1896) sank *Tallula* under *Tioga*. Janse (1931) used *atrifascialis* Hulst for his study of the genus. He summarized Hampson's comparison



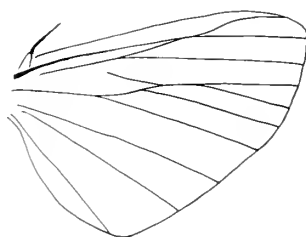
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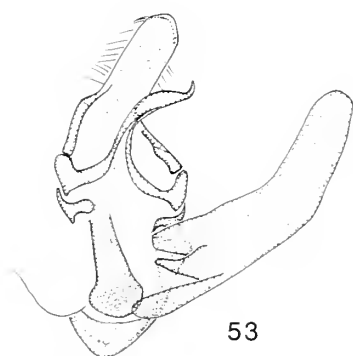
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Figs. 52–56. *Tallula atrifascialis* Hulst. 52. Female genitalia #287 MAS. 53. Male genitalia #383 MAS. 54. Male head #826 MAS. 55. Wings #287 MAS. 56. Aedeagus #287 MAS.

between *Tioga* and *Pococera* and discussed the validity of the wing venation characters as used by Hampson. Holland and Schaus (1925) placed most of the species under the genus *Tioga*. Munroe (1983) resurrected *Tallula* and placed *Tioga* as a junior synonym of *Tetralopha*.

Many of the species were already included due to their external similarity. It has 11 species (see Nomenclatural Summary), but I suspect that many are synonyms, because little or no variation was apparent in descaled structures. They differ only in size and wing pattern.

Tancoa Schaus, 1922

Figs. 57–62, 126

Tancoa Schaus, 1922:217.

Diagnosis. *Tancoa* has three autapomorphies found in the male genitalia: presence of *socii*, a membranous extension at the apex of the costa of valva, and a dorsocaudal extension from the tegumen (Fig. 59). Several homoplasious characters also diagnose this genus: a third segment of the maxillary palpus arising at the midpoint of the second segment, also occurring in *Mazdacis*; a sclerotized pattern on the eighth abdominal sternum, also occurring in *Chloropaschia*; absence of a medial lobe at base of valva, which is also absent in *Roeseliodes*, *Tallula*, *Phidotricha*, *Mediavia*, and the outgroup *Macalla*; juxtal arms do not extend to the costa of valva as in *Roeseliodes*, *Cecidipta*, *Carthara*, *Mediavia*, *Oneida*, *Dasyvesica*, *Deuterollyta*, *Accinctapubes*, *Bibasilaris*, *Anarnatula*, and *Lacalma*; and the ductus ejaculatorius terminal, also occurring in *Roeseliodes*.

Identification synopsis. This genus can be identified by narrow wings and lines or spots of dark scales basal to the medial line of the forewing (Fig. 126).

The genus *Tancoa* is the sister group of *Pococera*. See *Pococera* for a comparison of the two genera.

Type species. *Deuterollyta calitas* Druce, 1899, Biol. Cent. Amer., Ins. Lep.-Het. II: 547, by subsequent designation. Type locality. Bugaba, Panama (BMNH).

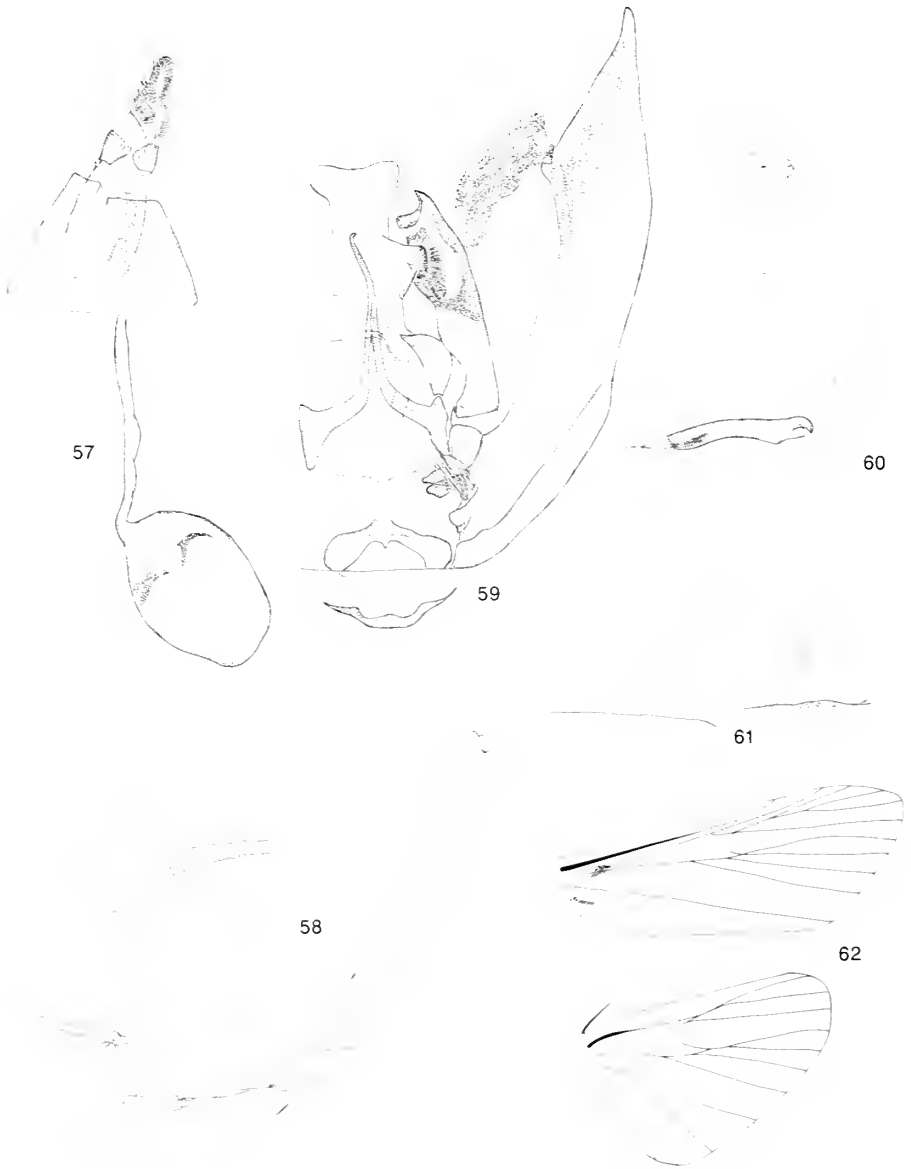
Species examined. *attenualis* (Hampson), *calitas* (Druce), *sphaerophora* (Dyar), *crinita* (Schaus), *erlupha* Schaus, *pallidifusa* (Dognin), *quiriguana* (Schaus).

Distribution. Mexico (Yucatan) to Peru and Brazil, with one record from Trinidad.

Biology. Two new species in the collection of Vitor O. Becker (Planaltina, Brazil) were reared one on *Emmotum nitens* Miers (Icacinaceae), and the other on *Qualea grandiflora* Martius (Vochysiaceae).

Remarks. Janse (1931) redescribed *Tancoa* and stated that the "genitalia are very peculiar and would place *Tancoa* in a group by itself." Its affinity was unknown to Janse. This study places *Tancoa* as the sister group to *Pococera*.

Most of the ten species in the genus are very similar externally and were already included in the genus (see Nomenclatural Summary). They can be distinguished by wing color and pattern; shape of the apex of the uncus, valva, socius, extension from the tegumen; scale tuft on the valva; and sclerotization of the eighth abdominal sternum. The extension from the scape and the length of the third segment of the maxillary palpus also may provide information at the species level.



Figs. 57–62. *Tancoa calitas* (Druce). 57. Female genitalia #837 MAS. 58. Male head #836 MAS. 59. Male genitalia #836 MAS. 60. Aedeagus #836 MAS. 61. Eighth abdominal tergum and sternum #836 MAS. 62. Wings #836 MAS.

Pococera Zeller, 1848

Figs. 63–69, 127

Pococera Zeller, 1848:874–875.

Tetralopha Zeller, 1848:879. **REVISED SYNONYMY.**

Lanihapse Clemens, 1860:206–207. **REVISED SYNONYMY.**

Hemimattia Lederer, 1863:347. **REVISED SYNONYMY.**

Benta Walker, 1863:112. **REVISED SYNONYMY.**

Auradisa Walker, [1866] 1865:1504. **REVISED SYNONYMY.**

Saluda Hulst, 1888:113. **REVISED SYNONYMY.**

Katona Hulst, 1888:113. **REVISED SYNONYMY.**

Loma Hulst, 1888:114. **REVISED SYNONYMY.**

Wanda Hulst, 1888:114. **REVISED SYNONYMY.**

Tioga Hulst, 1888:113. **NEW SYNONYMY.**

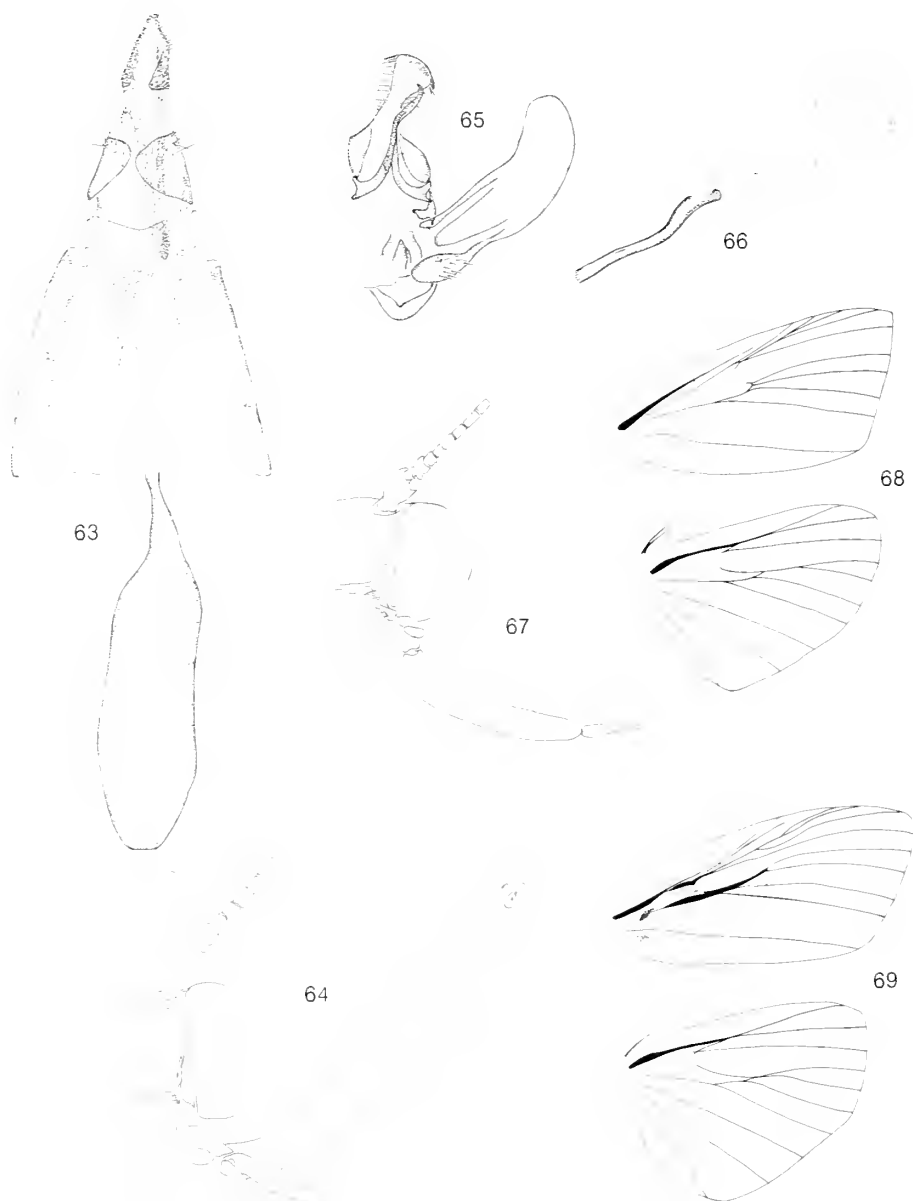
Attacapa Hulst, 1889:71. **REVISED SYNONYMY.**

Diagnosis. *Pococera* is diagnosed by a unique combination of homoplasious characters, usually a costal fold in the forewing of the male, a discocellular cell half or less than the length of forewing, also occurring in *Mazdacis*, 3A not coincident with 1A + 2A, as in *Roeseliodes*, *Tallula*, *Phidotricha*, *Oneida*, *Dasyvesica*, and *Anarnatula*, the tip of the tegumen sclerite as broad as the base, as in *Quadraforma* and *Phidotricha*, the base of juxta with the medial lobe long and pointed as in *Phidotricha*, *Milgithea*, *Accinctapubes*, *Bibasilaris*, *Anarnatula*, and *Toripalpus*, a single row of setae on the caudal end of uncus, as in *Cecidipta*, *Phidotricha*, and *Tallula*, and the width at the caudal end of the uncus wider than the width of the midpoint, as in *Cecidipta*, *Mediavia*, *Bibasilaris* and *Lacalma*.

Identification synopsis. *Pococera* can be identified by a wing pattern (Fig. 127) with the postmedial line extending to outer margin at M_2 and the postmedial line that is faintly present in the hindwing.

The sister group of *Pococera* is *Tancoa*, but they can easily be differentiated. *Pococera* has an elongated scape, and *Tancoa* does not. *Pococera* has the third segment of the maxillary palpus arising at the base of the second segment, and *Tancoa* has the third segment arising at the midpoint of the second segment. In the hindwing, $Sc+R_1$ and Rs are separate in *Tancoa*, but fused in *Pococera*. Setae at the caudal end of the uncus are a single row on *Pococera*, but in *Tancoa* the setae arise between the caudal end and half the length of the uncus. The width of the uncus at the caudal end is wider than the midpoint of the uncus in *Pococera*, but not wider in *Tancoa*. *Pococera* has a medial lobe at the base of the valva that is absent in *Tancoa*. The ductus ejaculatorius is terminal in *Tancoa* and subterminal in *Pococera*. The juxtal arms do not extend to the costa of the valva in *Pococera*, but extend beyond the costa in *Tancoa*. The medial lobe at the base of the juxta in *Pococera* is long and pointed, but small and round in *Tancoa*.

Type species. *Pococera gibella* Zeller, 1848, *ibid.* XI: 874, by monotypy. Type locality. S. del Rey: Sello, Brazil (HMB). *Tetralopha* Zeller, 1848, *ibid.* XI: 879. Type species: *T. militella* Zeller designated by Holland and Schaus, 1925, *Ann. Carn. Mus.* 16: 60. *Lanihapse* Clemens, 1860, *ibid.* 5: 206–207. Type species: *L. platanella* Clemens designated by Fletcher and Nye, 1984, *Generic Names of Moths of the World*,



Figs. 63–69. *Pococera militella* (Zeller). 63. Female genitalia #501 MAS. 64. Male head #838 MAS. 65. Male genitalia #838 MAS. 66. Aedeagus #838 MAS. 67. Female head #839 MAS. 68. Female wings #839 MAS. 69. Male wings #838 MAS.

5: 79. *Hemimattia* Lederer, 1863, *ibid.* 7: 347. Type species: *H. scortealis* Lederer, designated by Fletcher and Nye, 1984, *ibid.* 5: 68. *Benta* Walker, 1863, *ibid.* 27: 112. Type species: *B. expandens* Walker, 1863, by monotypy. *Auradisa* Walker, [1866] 1865, *ibid.* 34: 1504. Type species: *A. gelidalis*, by monotypy. *Saluda* Hulst, 1888, *ibid.* 4: 113. Type species: *Lanthaphe asperatella* Clemens, 1860, *ibid.* 5: 207, by original designation. *Katona* Hulst, 1888, *ibid.* 4: 113. Type species: *K. euphemella* Hulst, 1888, by original designation. *Loma* Hulst, 1888, *ibid.* 4: 114. Type species: *L. nephelotella* Hulst, 1888, by original designation. *Loma* Hulst, 1888, *ibid.* 4: 114. Type species: *L. nephelotella* Hulst, by original designation. *Wanda* Hulst, 1888, *ibid.* 4: 114. Type species: *Tetralopha baptisiella* Fernald, 1887, by original designation. *Tioga* Hulst, 1888, *ibid.* 4: 113. Type species: *Tetralopha aplastella* Hulst, by original designation. *Attacapa* Hulst, 1889, *ibid.* 5: 71. Type species: *Tetralopha callipeplella* Hulst, 1888, by monotypy.

Species examined. *aplastella* (Hulst), *asperatella* (Clemens), *basalis* (Jones), *callipeplella* (Hulst), *euphemella* (Hulst), *expandens* (Walker), *fusculotella* (Ragonot), *gelidalis* (Walker), *gibella* Zeller, *griseella* (Barnes & Benjamin), *humereella* (Ragonot), *iogalis* (Schaus), *maritimalis* (McDunnough), *melanogrammos* (Zeller), *militella* (Zeller), *provoella* (Barnes & Benjamin), *robustella* Zeller, *scortealis* (Lederer), *subcanalis* (Walker), *texanella* Ragonot, *tiltella* (Hulst).

Distribution. Southern areas of eastern and midwestern provinces of Canada to Brazil.

Biology. Most of the biological information on the species has been compiled by the Canadian Department of Agriculture (Raizenne, 1952; Prentice et al., 1965) as they are occasional pests of deciduous trees and conifers. The larvae have been reared on very diverse host plants from pines to legumes to oaks (see Table 2). Most of the species are colonial webbers and folders of leaves. Allyson (1977) conducted a larval study of nine species and described the habits. Studies on larvae feeding on sycamore (Thompson and Solomon, 1986) suggest multiple broods in *militella*.

Remarks. Hampson (1896) synonymized *Tetralopha* under *Pococera*. Holland and Schaus (1925) resurrected *Tetralopha* and designated the type species as *militella* Zeller. They did not study the type of *Pococera* and stated that *gibella* Zeller was not found "in any collection in the United States." Janse (1931) stated that he did see two specimens of *gibella* sent to him by the Berlin Zoological Museum, but he did not see the type, and the male sent to him lacked the head. He used a female specimen of *asperatella* Clemens as an example of *Tetralopha* because he did not have a specimen *militella* Zeller. Janse used Hampson's key to describe the difference between the two genera. Hampson used the absence of an extension from the scape in two species of *Pococera* to separate them from other species with a process. *Gibella* does have a process, but I found it to be short in comparison to that of *militella* after denuding the head. Hampson also used the presence of a deep furrow in the cell of the forewing of the male *Pococera*, but absent in *Tetralopha*. This furrow is present in species of *Tetralopha*, but it is not prominent as in *Pococera*. Hampson also used wing venation to separate the two genera, but the males of *Tetralopha* have a highly variable and deformed venation co-occurring with a costal fold.

This genus contains 44 species names (see Nomenclatural Summary) and has always been regarded as difficult at the species level. Some species can be recognized by wing pattern and color. A costal fold is present in males of most species, but is

Table 2. Genera and number of species of the *Pococera* complex reported to feed on each host-plant family (see Taxonomic Synopsis for further details).

Plant family	Moth genus	No. species
Aceraceae	<u>Pococera</u>	2
Amaryllidaceae	<u>Phidotricha</u>	1
Anacardiaceae	<u>Phidotricha</u>	1
	<u>Pococera</u>	1
Betulaceae	<u>Pococera</u>	1
Carpinaceae	<u>Pococera</u>	1
Combretaceae	<u>Phidotricha</u>	1
Corylaceae	<u>Pococera</u>	1
Ericaceae	<u>Pococera</u>	1
Euphorbiaceae	<u>Cecidipta</u>	1
Fabaceae	<u>Cacozelia</u>	1
	<u>Phidotricha</u>	1
	<u>Pococera</u>	11
Fagaceae	<u>Pococera</u>	4
	<u>Oneida</u>	2
	<u>Tallula</u>	1
Hamamelidaceae	<u>Pococera</u>	1
Icacinaceae	<u>Tancoa</u>	1
Juglandaceae	<u>Pococera</u>	1
Lauraceae	<u>Deuterollyta</u>	6
	<u>Accinctapubes</u>	1
Malvaceae	<u>Phidotricha</u>	1
Moraceae	<u>Cecidipta</u>	1
Pinaceae	<u>Pococera</u>	3
Platanaceae	<u>Pococera</u>	1
Poaceae	<u>Phidotricha</u>	1
Polygonaceae	<u>Toripalpus</u>	2
Rhamnaceae	<u>Pococera</u>	1
Rosaceae	<u>Phidotricha</u>	1
	<u>Pococera</u>	1
Rubiaceae	<u>Phidotricha</u>	1
Rutaceae	<u>Tallula</u>	2
Salicaceae	<u>Pococera</u>	1
Sapotaceae	<u>Milgitha</u>	1
Simaroubaceae	<u>Deuterollyta</u>	1
Ulmaceae	<u>Pococera</u>	2
Verbenaceae	<u>Phidotricha</u>	1
Vochysiaceae	<u>Tancoa</u>	1

lacking in two species. It is suspected that comparative dimensions of the female signa and male uncus may be useful at the species level. Heads of the males vary widely from having a definite extension from the scape to an extension that barely protrudes from the scape to one that is simple, as in females, and a long third segment of the maxillary palpus arising from the base of the second segment. It may be that larvae and pupae will provide reliable characters at the species level.

Species have been thought to be highly host specific, but in at least one case this has been shown to be untrue. Allyson (1977) reported that *asperatella* Clemens has been reared on *Acer*, *Ulmus*, *Fagus*, *Carya*, *Ostrya*, *Gleditsia* and *Rhus*.

Toripalpus Grote, 1877

Figs. 70–74, 128

Toripalpus Grote, 1877:265.

Diagnosis. This genus has one homoplasy, the corpus bursae lacks signa as in *Tallula*.

Identification synopsis. *Toripalpus* can be identified by a forewing pattern (Fig. 128) with the postmedial line extending from R5 toward the outer margin and toward the base of the wing after CuA₂ and a medial line that is twice curved. A faint spot on 1A of the hindwing is present near the margin.

Toripalpus is found at the base of the cladogram of the *Pococera* complex. See *Cacozelia*, which it resembles externally, and *Milgithea*, which it is closely related to, for comparisons with these genera.

Type species. *Toripalpus brevionatalis* Grote, 1877, *ibid.* 19: 265, by monotypy. Type locality. Texas, Colorado, USA (AMNH).

Species examined. *brevionatalis* Grote, *trabalis* Grote.

Distribution. *Trabalis* occurs from British Columbia south to New Mexico, and *brevionatalis* occurs only in Texas, Oklahoma, and Florida.

Biology. The following host plant information is available at the USNM: *brevionatalis* on *Eriogonum tomentosum* Michx. Benth. (Polygonaceae) from Florida, and *trabalis* on *Eriogonum fasciculatum* from southern California. Comstock and Dammers (1935) described the larva and pupa of *trabalis* Grote.

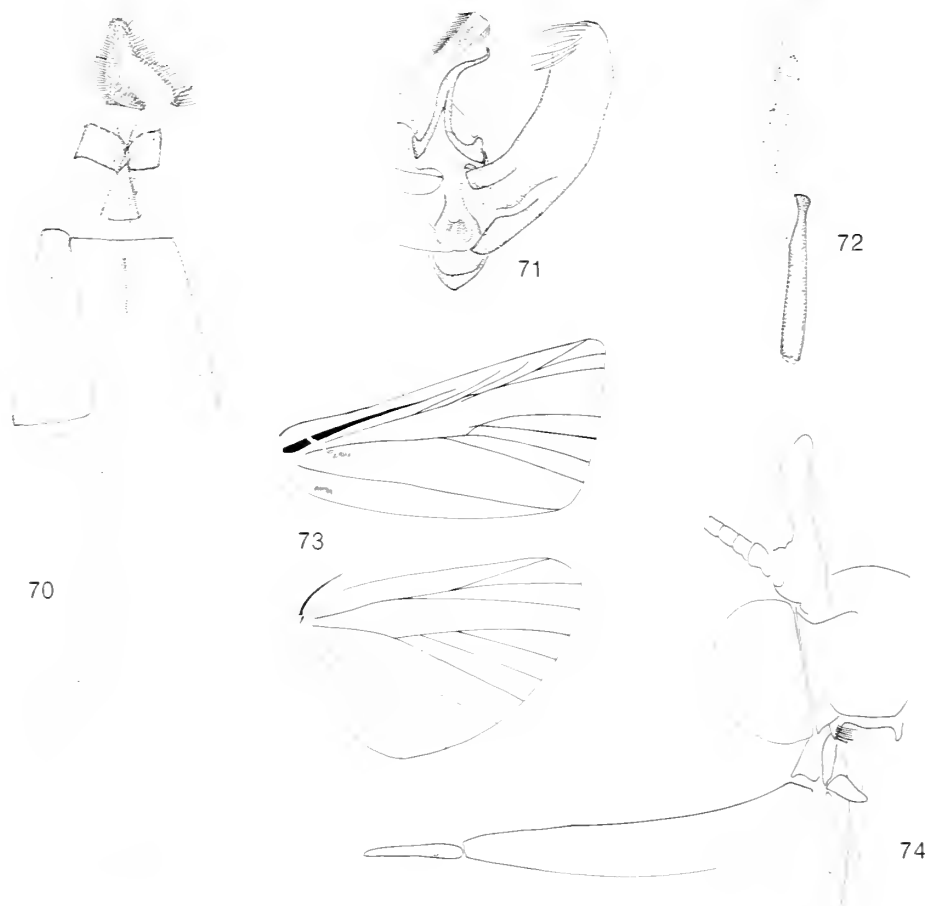
Remarks. *Toripalpus* was resurrected for two species that were previously placed in *Jocara* (see Nomenclatural Summary); it may be distinguished by wing pattern and color. Other differences may be seen in the shape of the clypeus, second and third segments of the maxillary palpus, and in the wing venation.

Pandoflabella, new genus

Figs. 75–79, 129

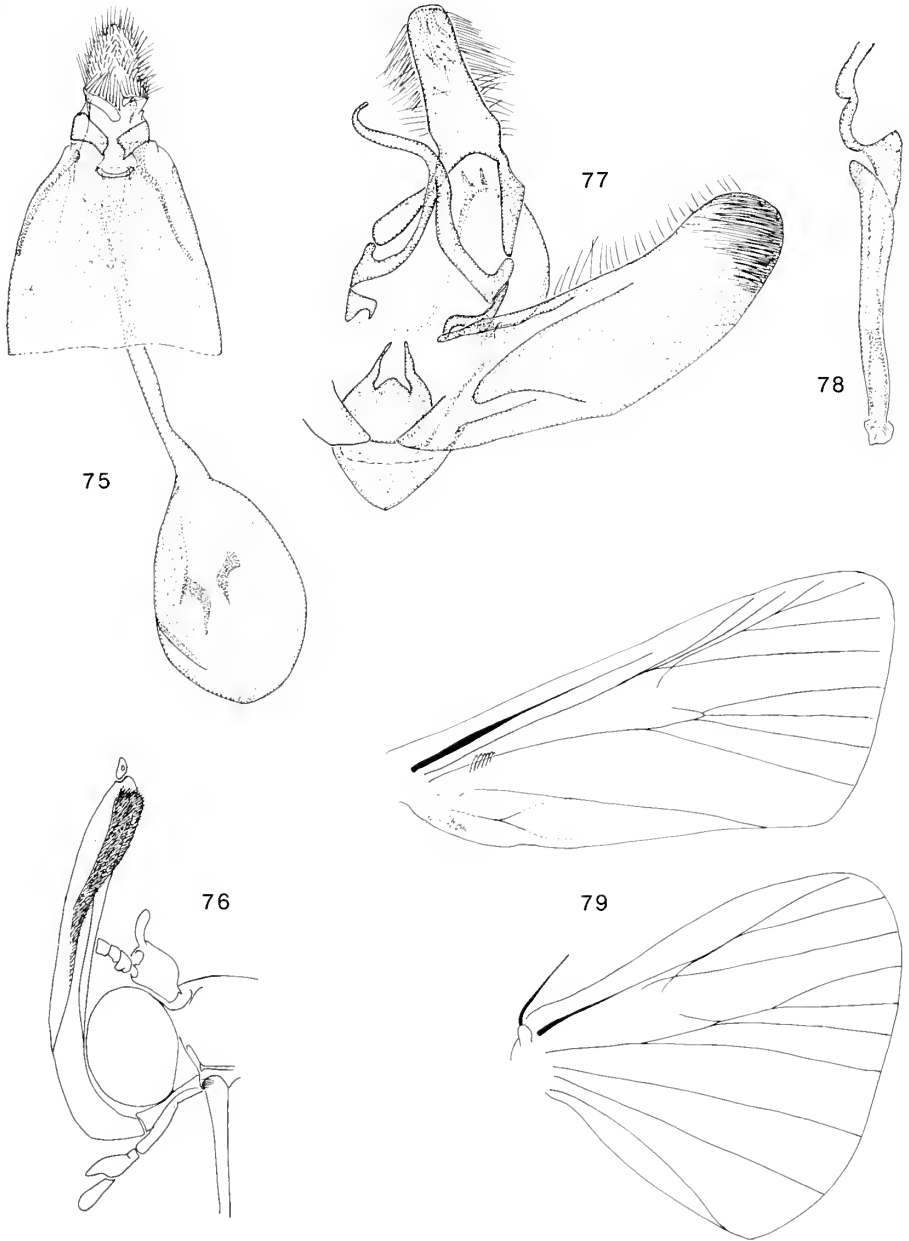
Diagnosis. *Pandoflabella* is characterized by an autapomorphy, the flabellate second labial segment (Fig. 76).

Identification synopsis. *Pandoflabella* can be identified by the forewing pattern (Fig. 129) with the postmedial line extending toward the outer margin from M₂ to CuA₂, and a patch of darker scales beyond the postmedial line above M₂. The medial line is bifurcate, turning sharply toward the base of the wing below CuA₂ and toward the base of the postmedial line about halfway along the width of the wing. The reniform spot is a small black curve.



Figs. 70-74. *Toripalpus* sp. 70. Female genitalia of *T. breviornatalis* Grote #441 MAS. 71. Male genitalia of *T. trabalis* Grote #150 MAS. 72. Aedeagus of *T. trabalis* #150 MAS. 73. Wings of *T. breviornatalis* #440 MAS. 74. Male head of *T. trabalis* #150 MAS.

Species of *Pandoflabella* can be confused with some species of *Chloropaschia* based on the wing pattern, but in *Pandoflabella* the medial line is bifurcate below CuA_2 then curving basally and toward the base of the postmedial line, while in *Chloropaschia* the medial line curves basally only below the reniform spot. In *Chloropaschia* the reniform spot is a dark line, but in *Pandoflabella* it is a black curve. In *Pandoflabella* the extension of the scape is longer than the base of the pedicel, but in *Chloropaschia* it is shorter than the base of the pedicel. The second segment of the labial palpus is flabellate in *Pandoflabella*, but simple with no modifications in *Chloropaschia*. The third segment of the maxillary palpus in *Chloropaschia* arises slightly below the apex of the second segment, but in *Pandoflabella* it arises at the base of the second segment. The first anal vein in *Chloropaschia* is present but absent in *Pandoflabella*. The



Figs. 75–79. *Pandoflabella olivescens* (Schaus). 75. Female genitalia #725 MAS. 76. Male head #724 MAS. 77. Male genitalia #724 MAS. 78. Aedeagus #724 MAS. 79. Wings #724 MAS.

ventral fold of the lamella antevaginalis in *Chloropaschia* is strongly bilobed but equal in width or weakly bilobed in *Pandoflabella*.

Description. Male head (Fig. 76): Extension of the scape longer than base of pedicel; third segment of the maxillary palpus arising at base of second segment. Wing (Fig. 79): Retinaculum a group of hooked setae just below Cu. CuP of forewing vein absent; 3A intersecting with 1A + 2A. Hindwing with Sc+R₁ and Rs coincident. Male genitalia (Fig. 77): Juxta with small median lobe; arms of juxta extended to base of costa; median lobe on valva a short, round nub; tegumen sclerite not reaching mid-ventral position, tip less broad than base; base of uncus with U-shaped sclerotized structure; vesica without cornuti. Female genitalia (Fig. 75): Fold of lamella antevaginalis not bilobed or weakly bilobed; two signa present.

Type species. *Pococera olivescens* Schaus, 1912, Ann. Mag. Nat. Hist. (8) 9: 659–660. Type locality. Costa Rica (USNM).

Species examined. *olivescens* (Schaus), *stenipteralis* (Hampson), *strigidiscalis* (Hampson), *fechina* (Schaus), *nigrilunalis* (Dognin), *nigriplaga* (Dognin), *remberta* (Schaus).

Distribution. Southern Mexico to the Matto Grosso in Brazil.

Biology. No information available.

Remarks. Most of the species in *Pandoflabella* were previously placed in *Auradisa*. *Auradisa* is now a junior synonym of *Pococera*.

Pandoflabella is composed of 11 species (see Nomenclatural Summary) and can be distinguished in the male genitalia by variation in shape of the juxta, shape of the valva, shape of the uncus, and the number of setae on the uncus. Other useful characters include the length of the extension of the scape and the nature of certain specialized structures on the ovipositor lobes, and length and width of the signa.

Etymology. The name of this genus is derived from the Latin *pando-* meaning “to spread” and the Latin *flabellum* (neuter) meaning “fan” in reference to its autapomorphy.

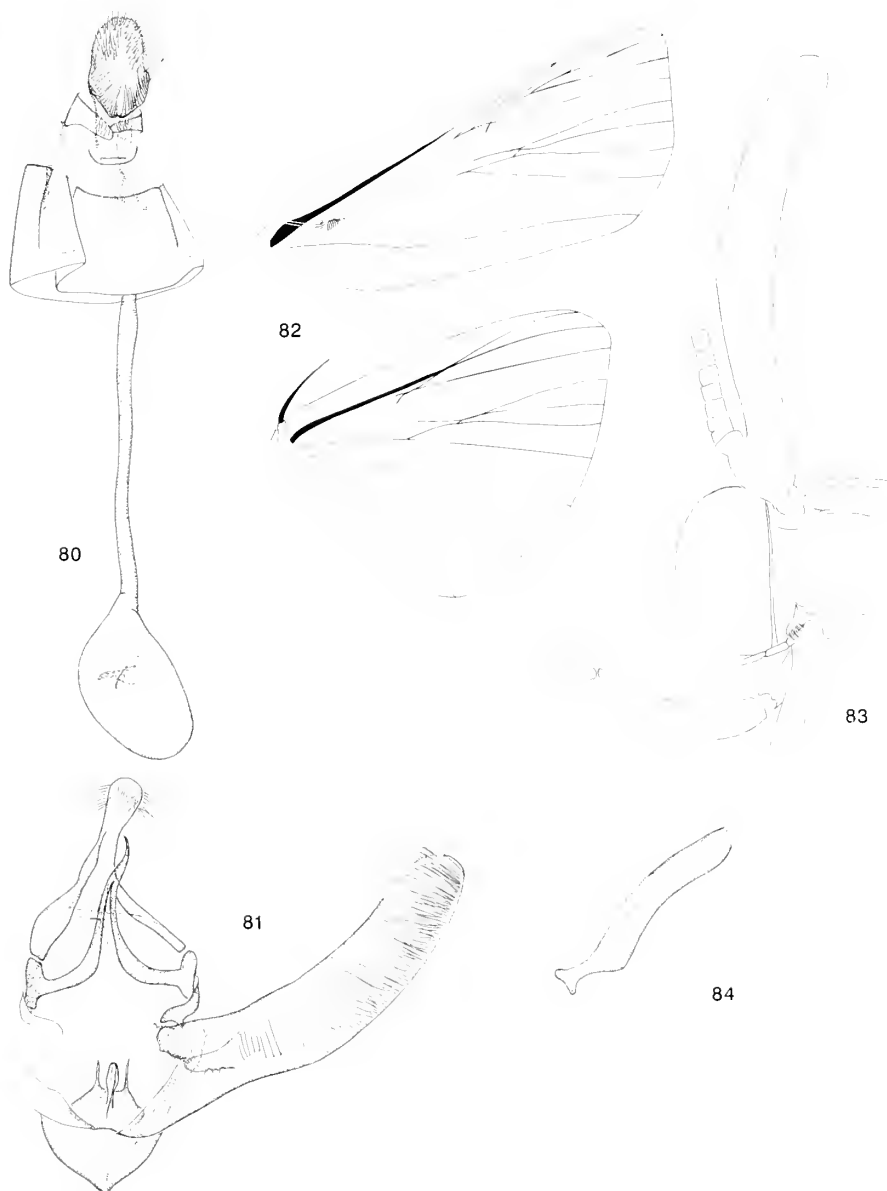
Bibasilaris, new genus

Figs. 80–84, 130

Diagnosis. *Bibasilaris* has one autapomorphy, the coecum of the aedeagus is bilobed (Fig. 84).

Identification synopsis. The forewing pattern (Fig. 130) has the postmedial line extending toward the outer margin at M₁ and curving toward the base of wing to the posterior margin. The reniform spot is a dark straight line. The hindwing postmedian line is present. *Carthara* is similar in wing length and basal color of the forewing to *Bibasilaris*. But *Carthara* has a second segment of the labial palpus concave, whereas it is simple in *Bibasilaris*. The frenulum hook is absent in *Carthara* and present in *Bibasilaris*. *Carthara* has an uncus that is not wider caudally than at the midpoint, but is wider caudally in *Bibasilaris*. *Carthara* has a juxta with a medial lobe that is small and round, and in *Bibasilaris* it is long and pointed. *Bibasilaris* also has the Rs of the hindwing more than half the length of the discocellular cell, whereas in *Carthara* it less than half the length.

Description. Male head (Fig. 83): Scape extension longer than base of pedicel; second segment of labial palpus simple, no modifications; third segment of maxillary



Figs. 80–84. *Bibasilaris trisulcata* (Warren). 80. Female genitalia #229 MAS. 81. Male genitalia #228 MAS. 82. Wings #228 MAS. 83. Male head #228 MAS. 84. Aedeagus #228 MAS.

palpus at apex of second segment. Wing (Fig. 82): Retinaculum a frenulum hook. CuP of forewing absent; 3A intersecting 1A + 2A. Hindwing with Sc+R₁ and Rs coincident. Male genitalia (Figs. 81, 84): Juxta with elongated median lobe; juxtal arms not reaching costa; median lobe on valva short, round nub; tegumen sclerite not reaching midventral position, tip narrower than base; base of uncus with U-shaped sclerotized structure; vesica without cornuti. Female genitalia (Fig. 80): Fold of lamella antevaginalis not bilobed; two signa present.

Type species. *Homura trisulcata* Warren, 1891, Ann. Mag. Nat. Hist. (6)7: 434. Type locality. Rio de Janeiro, Brazil (BMNH).

Species examined. *erythea* (Druce), *trisulcata* (Warren).

Distribution. Guatemala to southeastern Brazil.

Biology. No information available.

Remarks. The two species included here (see Nomenclatural Summary) were previously placed in *Locastra*, an Old World genus. Length of the wing averages 1.5 cm.

Species are distinguished by external wing morphology and the shape of the uncus in the male genitalia.

Etymology. The genus name is derived from the Latin *bi*—meaning “two,” and from the Latin *basilaris* (feminine) meaning at the “base.”

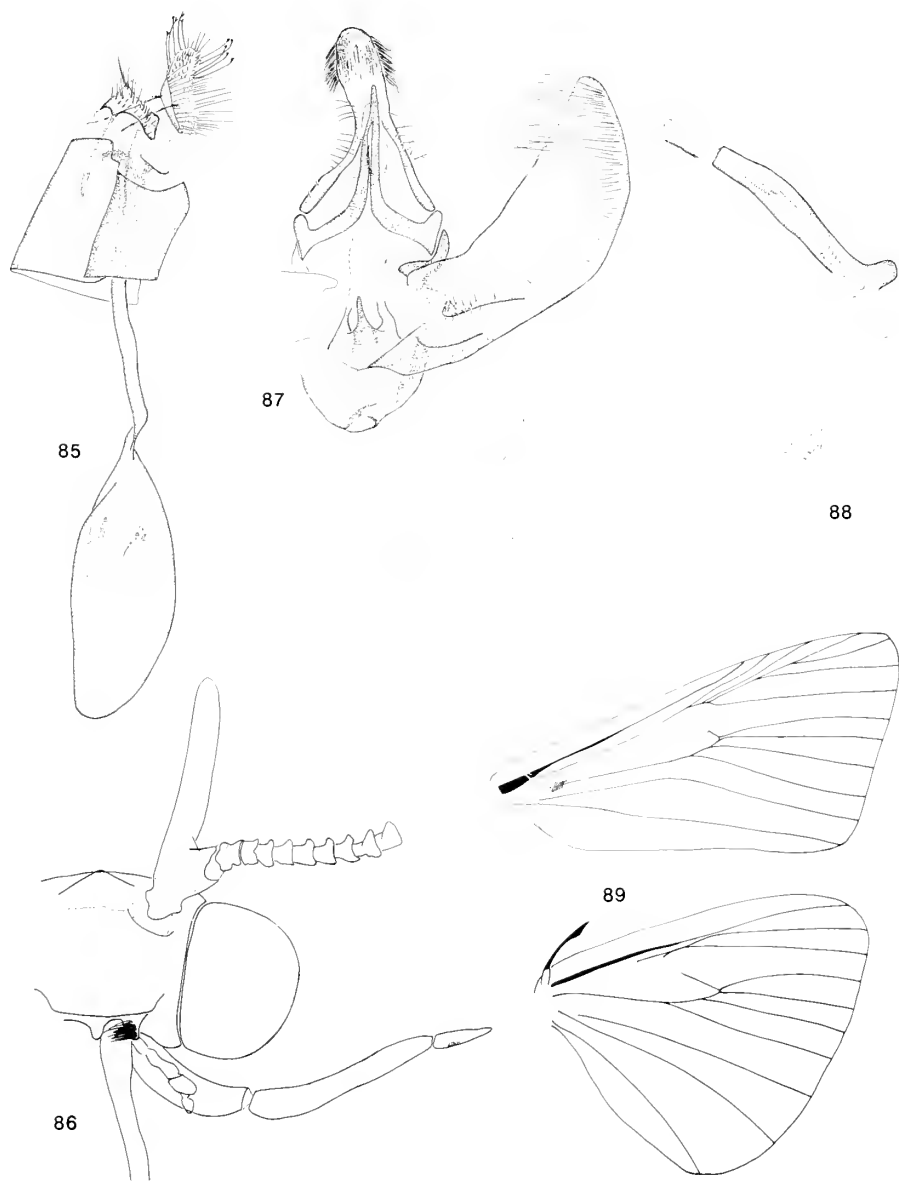
Accinctapubes, new genus

Figs. 85–89, 131

Diagnosis. *Accinctapubes* has two autapomorphies, a male frenulum that is bulbous at tip (Fig. 89); and ovipositor lobes with some spatulate setae, that are trifurcate distally (Fig. 85).

Identification synopsis. *Accinctapubes* can be identified by the forewing pattern (Fig. 131) with the postmedial line curving toward the outer margin at M₁. Species are sexually dimorphic, the males with white patches of scales, and the females without. The median line and reniform spot are not prominent. The hindwing post-medial line is prominent from the costal margin to 1A.

Accinctapubes is the sister group of the *Cecidipta-Roeseliodes* clade. Species of *Accinctapubes* are approximately midway in wing length between *Cecidipta* and *Roeseliodes* although some females of *Accinctapubes* approach the wing length of some *Cecidipta* males. Fresh specimens of *Accinctapubes* have the base of the forewing green, but this area is beige or white in *Cecidipta*. The apex of the male frenulum in *Cecidipta* is tapered, but in *Accinctapubes* it is bulbous. In the male genitalia *Cecidipta* has a tegumen sclerite that extends beyond the midventral position, whereas in *Accinctapubes* it does not reach a midventral position. The tip of the tegumen sclerite is narrower than the base in *Accinctapubes*, but in *Cecidipta* the tip is broader than the base. *Cecidipta* lacks a sclerotized structure at the base of the uncus, but it is present in *Accinctapubes*. In *Accinctapubes* the caudal end of the uncus is not wider than the midpoint and setae extend to half the length of the uncus; whereas in *Cecidipta* the uncus is wider at the caudal end and setae are in a single row at the caudal end. The arms of the juxta in *Cecidipta* do not extend to the costa of the valva and in *Accinctapubes* they extend beyond the costa. In female *Accinctapubes* some



Figs. 85–89. *Accinctapubes albifasciata* (Druce). 85. Female genitalia #883 MAS. 86. Male head #867 MAS. 87. Male genitalia #867 MAS. 88. Aedeagus #867 MAS. 89. Wings #867 MAS.

of the setae on the ovipositor lobes are spatulate then trifurcate distally, but all setae are simple in *Cecidipta*.

Description. Male head (Fig. 86): Scape extension longer than base of pedicel; segment of the second labial palpus simple, no modifications; third maxillary segment arising from base of second. Wing (Fig. 89): Retinaculum a frenulum hook; forewing CuP absent; 3A intersecting 1A + 2A; hindwing with Sc+R₁ and Rs not coincident. Male genitalia (Fig. 87): Juxta with elongated median lobe; juxtal arms not extending to costa; median lobe short, round nub; tegumen sclerite not reaching midventral position, tip narrower than base; base of uncus with U-shaped sclerotized structure; vesica without cornuti. Female genitalia (Fig. 85): Fold of lamella antevaginalis not bilobed or weakly bilobed; two signa present.

Type species. *Cecidiptera* [sic] *albifasciata* Druce, 1902, Ann. Mag. Nat. Hist. (7) 9:325. Type locality. Sarayacu, Ecuador (TMP).

Species examined. *albifasciata* (Druce), *chionopheralis* (Hampson), *apicalis* (Schaus).

Distribution. Southern Mexico to Paraguay and Brazil.

Biology. *Albifasciata* has been reared on avocado (Lauraceae) (Dyar, 1912). In Trinidad the species is known as the "avocado moth," and "The caterpillars are gregarious and live in nests made by webbing leaves and branches with tough silk" (Kaye and Lamont, 1927 from Williams, 1922, p. 62: "Fruit Cultivation in Trinidad" "Pests of Avocados: Webbing Caterpillars").

Remarks. Two newly included species were previously placed in the Old World genus *Stericta*.

Accinctapubes has four species (see Nomenclatural Summary), but there is at least one new species in the USNM collection. Species are distinguished by the presence or absence of a thick patch of setae on the dorsal surface of the forewing and the shape of the lobe at the base of the valva in the male genitalia.

Etymology. The generic name is derived from the Latin *accinctus* meaning "well-equipped," and from the Latin *pubes* (feminine) meaning "private parts," in an anthropomorphic sense to its two unique autapomorphies, a bulbous frenulum in the male and some trifurcate setae on the female ovipositor.

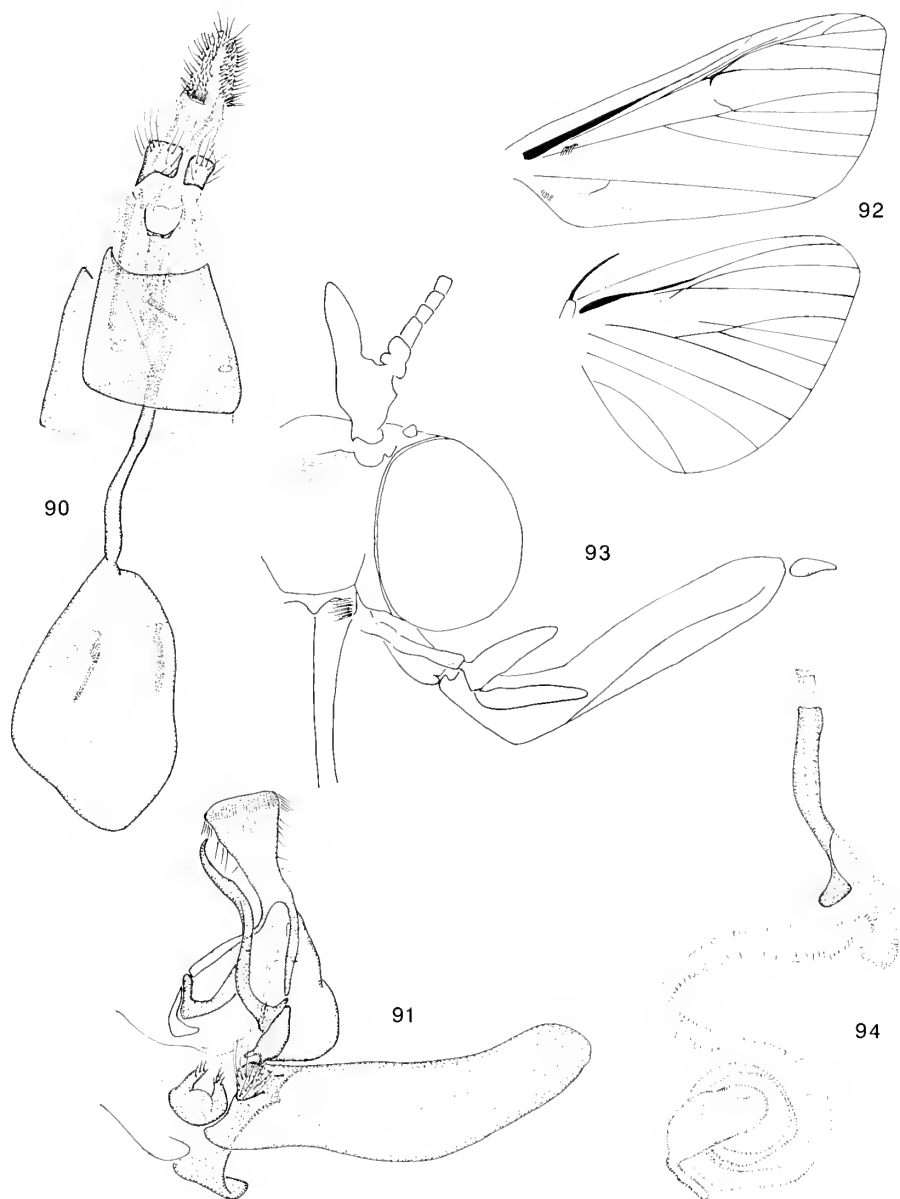
Mediavia, new genus

Figs. 90–94, 132

Diagnosis. *Mediavia* has two unique autapomorphies: the origin of R₂ distal to the discocellular cell (Fig. 92), and the presence of a lobe at the base of valva adjacent to the costa extending midventrally to the juxta (Fig. 91). Two homoplasies also diagnose this genus: a medial lobe is absent at the base of the valva, as in *Roeseliodes*, *Tallula*, *Phidotricha*, and *Tancoa* and the outgroup *Macalla*; and an uncus wider at the caudal end than the midpoint, also occurring in *Cecidipta*, *Pococera*, *Bibasilaris*, and *Lacalma*.

Identification synopsis. *Mediavia* can be identified by the forewing pattern (Fig. 132) with the postmedial line curving toward the costa of the wing above CuA₁ and below CuA₁ extending to base of wing.

The sister group of *Mediavia* is *Deuterollyta*, and externally they can be distinguished by the shape of the postmedial line in the forewing. In *Deuterollyta* the postmedial line above R₅ shifts abruptly toward the base of the wing and in *Mediavia*



Figs. 90–94. *Mediavia discalis* (Hampson). 90. Female genitalia #230 MAS. 91. Male genitalia #890 MAS. 92. Wings #890 MAS. 93. Male head #890 MAS. 94. Aedeagus #890 MAS.

it curves toward the costa of the wing above CuA_1 . *Deuterollyta* has CuP present in the forewing but it is absent in *Mediavia*. A frenulum hook is present in *Deuterollyta* but absent in *Mediavia*. $Sc+R_1$ and R_s in the hindwing are fused in *Deuterollyta* but separate in *Mediavia*. The uncus at the caudal end is as wide as the width at midpoint in *Deuterollyta*, but in *Mediavia* the caudal end is wider than the width at the midpoint. The medial lobe at the base of the valva is absent in *Deuterollyta* but present in *Mediavia*.

Description. Male head (Fig. 93): Scape extension longer than base of pedicel; second segment of labial palpus concave; third segment of maxillary palpus at base of second segment. Wing (Fig. 92): Retinaculum a group of hooked setae below Cu . Forewing with CuP absent; $3A$ intersecting with $1A + 2A$. Hindwing with $Sc+R_1$ and R_s separate. Male genitalia (Fig. 91): Juxta with small median lobe; juxtal arms not reaching costa of valva; tegumen sclerite not reaching midventral position, tip narrower than base; base of uncus with U-shaped sclerotized structure. Female genitalia (Fig. 90): Lamella antevaginalis fold not bilobed or weakly bilobed; two signa present.

Type species. *Jocara discalis* Hampson, 1906, Ann. Mag. Nat. Hist. (7) 17: 133. Type locality. St. Jean Maroni, French Guiana (BMNH).

Species examined. *aciusa* (Schaus), *bevnoa* (Schaus), *discalis* (Hampson), *dissimilis* (Warren), *eadberti* (Schaus), *glaucinalis* (Hampson), *grenvilalis* (Schaus), *hermengilda* (Schaus), *internigralis* (Dognin), *longistriga* (Schaus), *phaebadia* (Schaus), *soteris* (Schaus), *vimina* (Schaus), *zenoa* (Schaus).

Distribution. Northeastern Mexico south to Curitiba, Brazil. Apparently not present in the Caribbean.

Biology. No information available.

Remarks. The species included in *Mediavia* were previously placed primarily in *Stericta* and *Jocara*.

Mediavia has 18 species (see Nomenclatural Summary). The species can be distinguished by prominent scale color and pattern, variation of the shape of the lobe adjacent to the costa at the base of the valva, and the length of the extension of the scape.

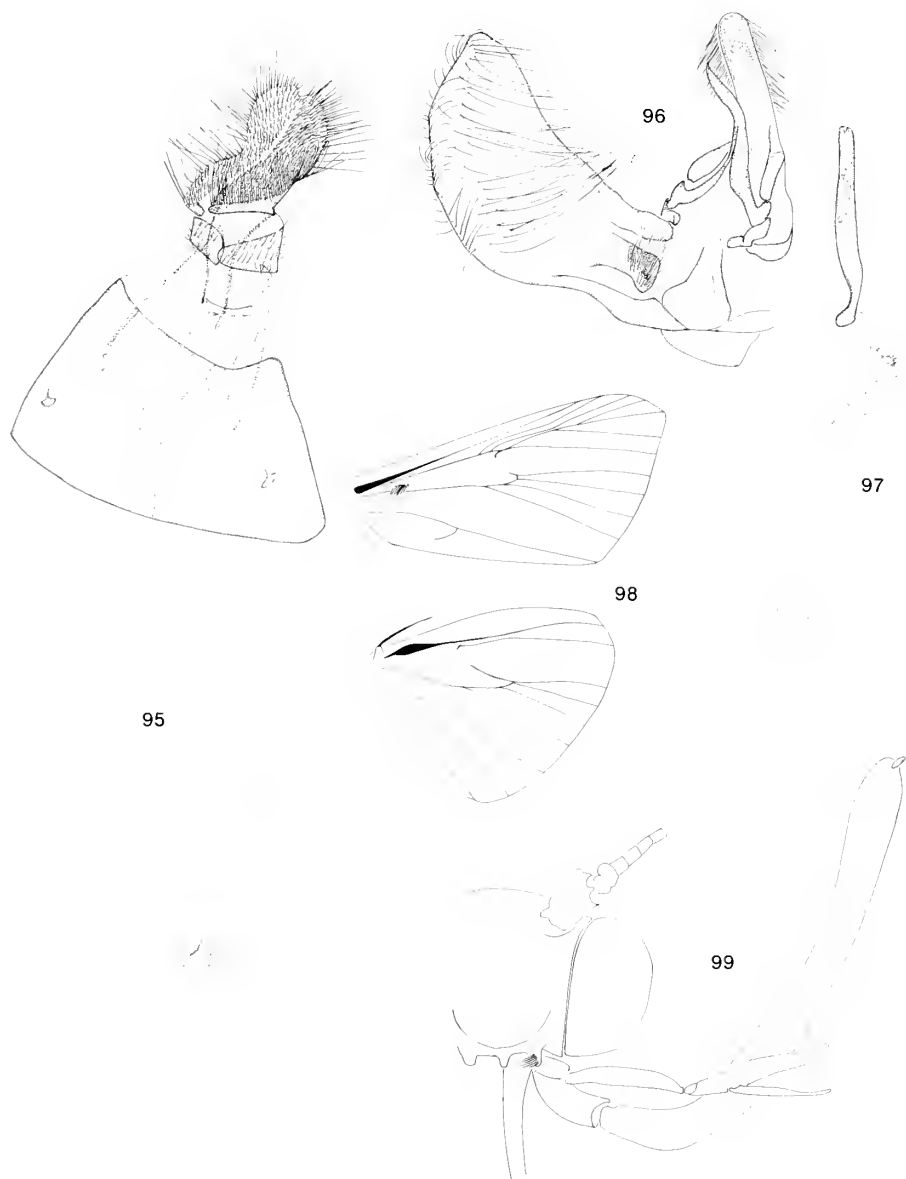
Etymology. This genus name is derived from the Latin *media via* meaning "middle of the road" in reference to one of its autapomorphies, a lobe extending medially toward the juxta.

Quadraforma, new genus

Figs. 95–99, 133

Diagnosis. *Quadraforma* has one autapomorphy, a long and square-shaped medial lobe at the base of valva (Fig. 96). It is also distinguished by two homoplasious characters, a tubular second segment of the labial palpus, also occurring in *Bibasilaris*, *Dasyvesica*, *Mazdacis*, *Milgithea*, *Pococera*, *Tancoa*, *Cacozelia*, and *Lacalma*, and the tip of tegumen sclerite as broad as base, as in *Phidotricha* and *Pococera*.

Identification synopsis. *Quadraforma* can be identified by a forewing pattern (Fig. 133) with the basal band usually present in males. The medial line bifurcates just below the reniform spot, one line extending to the posterior margin and the other to base of the postmedial line. The reniform spot is a small line.



Figs. 95–99. *Quadraforma obliqualis* (Hampson). 95. Female genitalia #892 MAS. 96. Male genitalia #891 MAS. 97. Aedeagus #891 MAS. 98. Wings #891 MAS. 99. Male head #891 MAS.

Chloropaschia is the sister group of *Quadraforma*. Externally, species of *Chloropaschia* and *Quadraforma* can be distinguished by a medial line that curves basally in *Chloropaschia*, whereas the medial line bifurcates, one line extending to the posterior margin and the other to the base of the postmedial line in *Quadraforma*. *Chloropaschia* has a simple second segment of the labial palpus and *Quadraforma* has a tubular second segment of the labial palpus. In *Chloropaschia* the third segment of the maxillary palpus arises at the apex of the second segment, but in *Quadraforma* it arises at the base of the second segment. In *Chloropaschia* Sc+R₁ and Rs of the hindwing are fused, and in *Quadraforma* they are separate. *Quadraforma* lacks the sclerotized pattern on the eighth abdominal sternum that is present in *Chloropaschia*.

Description. Male head (Fig. 95): Extension of scape not extending beyond base of pedicel; second segment of labial palpus tubular; third segment of maxillary palpus arising from base of second segment. Wing (Fig. 96): Retinaculum a group of hooked setae just below Cu. Forewing with CuP absent; 3A intersecting with 1A + 2A. Hindwing with Sc+R₁ and Rs separate. Male genitalia (Fig. 96): Juxta with small medial lobe; juxtal arms extended to a point perpendicular to costa of valva; tegumen sclerite not reaching midventral position, tip as broad as base; uncus base with U-shaped sclerotized support; vesica without cornuti. Female genitalia (Fig. 95): Fold of lamella antevaginalis strongly bilobed; two signa present.

Type species. *Stericta obliquialis* Hampson, 1906, Ann. Mag. Nat. Hist. (7) 17:145. Type locality, Yungas-la-Paz, Bolivia (BMNH).

Species examined. *maroniensis* (Hampson), *mianalis* (Felder & Rogenhofer), *obliquialis* (Hampson), *seminigrilis* (Hampson).

Distribution. Sinaloa, Mexico to southern Brazil. Apparently not present in the Caribbean.

Biology. No information available.

Remarks. Most of the species in *Quadraforma* were previously placed in the Old World genus *Stericta*.

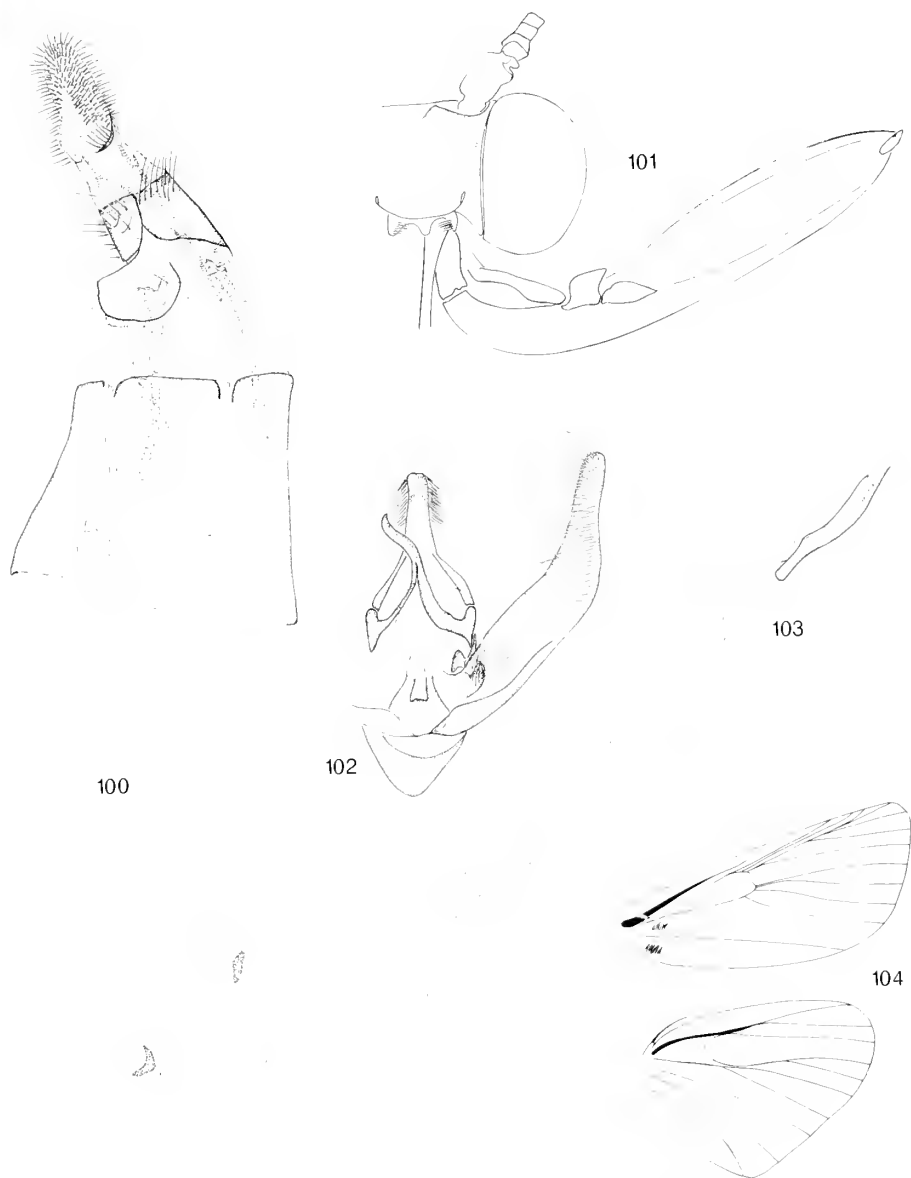
Quadraforma has four species (see Nomenclatural Summary) that can be distinguished by scale color and size. *Quadraforma obliquialis* exhibits much variation externally and in the labial and maxillary palpi, and may be a complex of sibling species.

Etymology. The genus name is derived from the Latin *quadra* meaning "square" and the Latin *forma* (feminine) meaning "shape" referring to the square-shaped lobe at the base of the valva.

Mazdacis, new genus

Figs. 100–104, 134

Diagnosis. *Mazdacis* has one autapomorphy, the lateral ridges on the frons extended medially to base of the clypeus (Fig. 101). The genus is also diagnosed by a combination of homoplasious characters: the third segment of the maxillary palpus arising at the midpoint of the second segment, as in *Tancoa*, the second segment of the labial palpus tubular, as in *Dasyvesica*, *Quadraforma*, *Cacozelia*, *Tancoa*, *Pococera*, *Milgithea* and *Lacalma*; a frenulum hook present, as in *Milgithea*, *Deuterollyta*, *Bibasilaris*, *Accinctapubes*, *Anarnatula*, *Toripalpus* and *Macalla*; the discocellular cell



Figs. 100–104. *Mazdacis consimilis* (Dognin). 100. Female genitalia #450 MAS. 101. Male head #449 MAS. 102. Male genitalia #449 MAS. 103. Aedeagus #450 MAS. 104. Wings #449 MAS.

half the forewing length or less, as in *Pococera*; and the tip of tegumen sclerite broader than the base, as in *Cecidipta*.

Identification synopsis. *Mazdacis* can be identified by a sheen to the entire body particularly the wings and a forewing pattern (Fig. 134) with the postmedial line extending toward the outer margin to M_2 and M_3 and then extending toward the base of the wing until CuA_2 where the line extends toward the posterior margin. A band extends from the medial line at CuP to the base of wing. The reniform spot is faint and curved.

Mazdacis is the sister group to the *Chloropaschia*, *Quadraforma* clade. *Mazdacis* can be distinguished from *Chloropaschia* by the second segment of the labial palpus that is simple in *Chloropaschia*, but tubular in *Mazdacis*. The third segment of the maxillary palpus arises slightly below the apex of the second segment in *Chloropaschia*, but is at the midpoint of the second segment in *Mazdacis*. The frenulum hook is absent in *Chloropaschia*, but present in *Mazdacis*. The discocellular cell is more than half as long as the length of the forewing in *Chloropaschia*, but half as long or less than the forewing length in *Mazdacis*. CuP of the forewing is absent in *Mazdacis*, but present in *Chloropaschia*. In the hindwing, $Sc+R_1$ and Rs are fused at one point in *Chloropaschia*, but separate in *Mazdacis*. The tip of the tegumen sclerite is narrower than the base in *Chloropaschia*, but broader than the base in *Mazdacis*. In *Chloropaschia* the ventral fold of the lamella antevaginalis is strongly bilobed, but in *Mazdacis* it is equal in width or weakly bilobed.

Description. Male head (Fig. 101): Scape extension not longer than base of pedicel; second segment of labial palpus tubular; third segment of maxillary palpus arising at midpoint of second segment. Wing (Fig. 104): Retinaculum a frenulum hook. Forewing with CuP absent; $3A$ intersecting with $1A + 2A$. Hindwing with $Sc+R_1$ and Rs coincident. Male genitalia (Fig. 102): Juxta with small median lobe; juxtal arms reaching costa of valva; median lobe on valva a short, round nub; tegumen sclerite not reaching midventral position, tip broader than base; uncus base with U-shaped sclerotized structure; vesica without cornuti. Female genitalia (Fig. 100): Fold of lamella antevaginalis not bilobed or weakly bilobed; two signa present.

Type species. *Epipaschia consimilis* Dognin, 1911, Het. Nouv. L'amer. Sud, Fasc. III: 64. Type locality. St. Laurent du Maroni, French Guiana (USNM).

Species examined. *flavomarginata* (Druce), *consimilis* (Dognin), *zenoa* (Schaus).

Distribution. Central Brazil to French Guiana and Guyana then west to Peru.

Biology. No information available.

Remarks. The species presently included in this genus were previously in several genera. *Mazdacis* has three species (see Nomenclatural Summary). They differ in the shape of the male valva, the modification of the maxillary palpi, and the size of the ridge on the head of the male.

Etymology. The generic name is derived from the Persian Mazda, "god of light" referring to the shiny surface of the adult moths.

CLADISTIC ANALYSIS

Monophyly of the Pococera complex. After the survey of the genera of the Epipaschiinae, the *Pococera* complex was found to be monophyletic based on two synapomorphies, the presence of a saccus in the male genitalia and the distinctly narrowed

ductus bursae in the female genitalia. The saccus is elongate, bulbous and curved up toward the coecum of the aedeagus and this condition is unique in the Pyralidae, but occurs in the Crambidae (B. Landry, pers. comm.) and in other lepidopteran groups. The entire vinculum may curve up toward the base of the aedeagus in other epipaschiines and pyralids, but in those groups it is not an evagination of the saccus. The term "saccus" is commonly used to describe the anteromesial point of the vinculum, but in the epipaschiines the saccus is also an evagination. In the female genitalia the ductus bursae near the ostium bursae is always less than half as wide as the posterior margin of the seventh segment, in contrast to a ductus that is at least half as wide as the posterior margin of the seventh segment as occurs in other epipaschiines (including *Lacalma* and *Macalla*), other Pyralidae (especially the epipaschiine sister group Phycitinae) and some Crambidae. The narrow ductus bursae does occur in some pyralines and crambids. The distribution of this character in the crambids is not well known.

Re-examination of the genera and delimitation of the terminal taxa. To develop generic concepts, synapomorphies (unique states that do not occur in the outgroups) were sought to define the smallest groups of species. Tentative generic concepts based on the synapomorphies of species groups were tested with additional dissection of species and preliminary cladistic analyses. Groups of species that did not have synapomorphies were consolidated with near relatives. The results of this analysis formed the basis of the re-classification of the genera of the *Pococera* complex as described in the Taxonomic Synopsis discussion following the phylogenetic analysis.

Previous concepts of the importance of some characters over others were not taken into consideration. Characters such as wing pattern, color, and wing venation, upon which the old generic concepts were based, were not utilized during the development of new generic concepts. Wing pattern and color were not used as characters for this cladistic analysis (Solis, 1991), and previous concepts of wing venation were for the most part found to be unreliable (Janse, 1931, and in reference to Hampson, 1896). Many of the smaller genera that were externally distinctive, such as *Anarnatula*, were supported by this analysis. The larger genera (e.g., *Jocara* and *Stericta*) usually consisted of unnatural groups of species. These genera formerly included many species now placed in a wide variety of other genera (see original combinations, Nomenclatural Summary). In the case of *Stericta*, the type species, *divitalis* Guenée from Indo-Australia, was dissected and found not to belong to the *Pococera* complex.

The Nomenclatural Summary lists genera and species that are only provisionally placed in the *Pococera* complex. Most of the species listed were not dissected to verify their placement due to time and other constraints, such as inaccessibility of types. Many species appear, after perusal of external characters, to be synonyms of other species. Some genera and associated species that were not included in the analysis for a number of reasons are included in the Nomenclatural Summary under *Incertae sedis*. For example, the description of the genus *Jocara* was based on one female from the Dominican Republic. Only one other specimen, another female, from Haiti was located. The type specimens of *Anaeglis* and *Homura* described by Lederer could not be located at their expected repositories in Berlin and Vienna.

Outgroups. Historically, epipaschiines have been hypothesized to be closely related either to the pyralines or phycitines. The preliminary phylogenetic analysis of the Pyralidae (Solis and Mitter, 1992) placed the Epipaschiinae as sister group to the

Phycitinae. But the Phycitinae are a highly derived group and correlation of characters for the purpose of polarization was difficult. In preliminary analyses the pyraline genus *Herculia* was used as an outgroup, but it too was divergent enough that the characters of the *Pococera* complex could not be polarized. Therefore *Macalla* (*sensu stricto*), a genus in the Epipaschiinae but outside the *Pococera* complex, was chosen as the outgroup. *Macalla* was used because extensive material was available and because it had been studied in-depth at the species level (Howard and Solis, 1989). *Macalla* (*sensu lato*) is historically a "waste basket," and a survey of some species in *Macalla* outside the Western Hemisphere showed that it is not monophyletic. For the purpose of this study *Macalla* is restricted to *noctuiipalpus* Dognin, *thyrsisalis* Walker, *arctata* Druce, and *hyalinalis* Amsel. This group of species share a juxta that is almost completely bifurcate and highly sclerotized (Fig. 107) and includes the type species, *Macalla thyrsisalis* Walker, from Honduras.

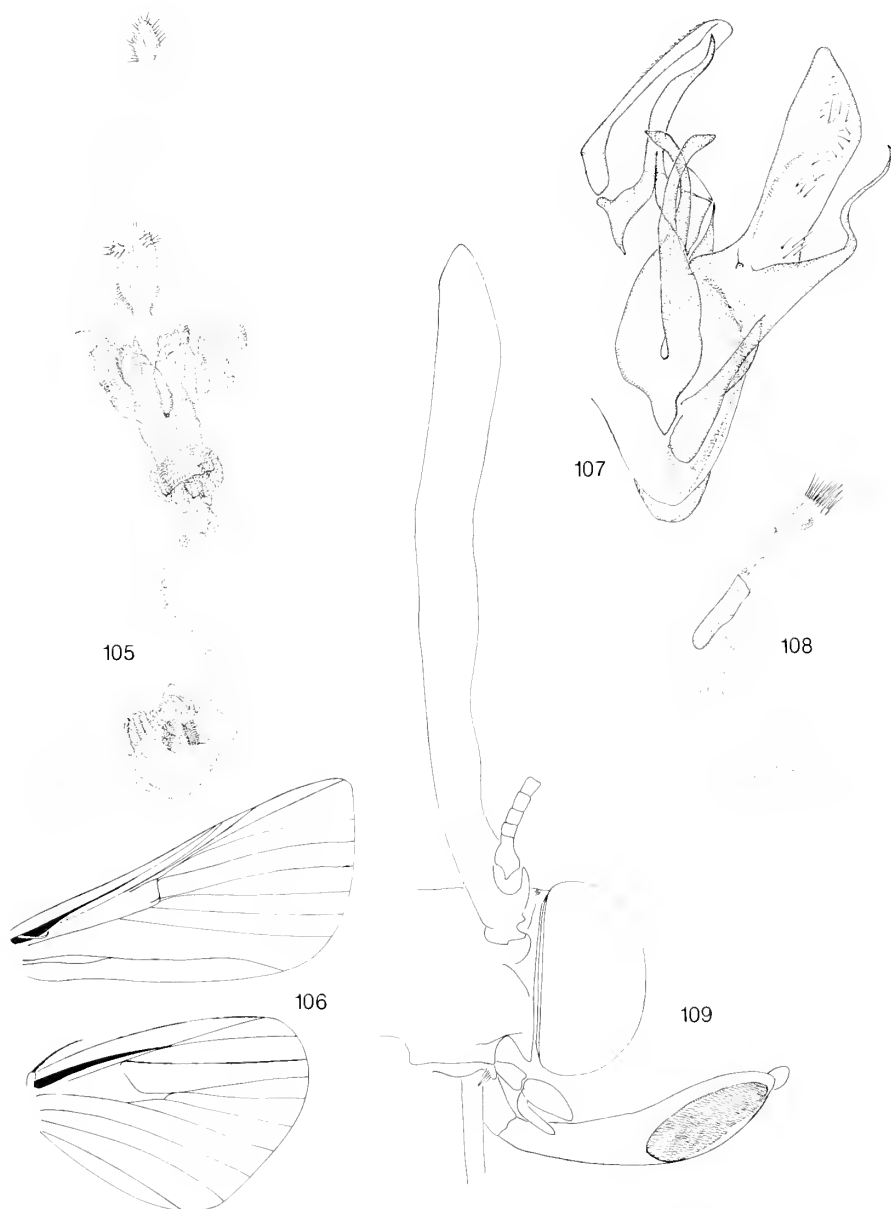
However, *Macalla* was also suspected of being a highly derived group based on the worldwide survey of the genera of the Epipaschiinae. *Lacalma*, a well-defined genus, was then added to the analysis because the survey and studies at the species level indicated a closer affinity to the ground plan of the *Pococera* complex than *Macalla*. Janse (1931) included four species in *Lacalma*. The genus is Indo-Australian in distribution and defined by an expanded vinculum with coremata (Fig. 111) in the male genitalia (Janse, 1931).

The exact relationship of *Macalla* and *Lacalma* to each other and to the group being revised was not investigated, since this would require a revision of the entire subfamily on a world basis. There is some evidence that *Macalla* is more basal to the epipaschiines than *Lacalma*. *Macalla* lacks a tegumen "sclerite" as in other subfamilies which puts forth the possibility that *Macalla* may be basal to all epipaschiines including the *Pococera* complex. Also, the signum in *Macalla* is scobinate and flat as in most phycitines, the sister group to the epipaschiines. The signa in the phycitines are variable but are never scobinate and spinelike as in the *Pococera* complex.

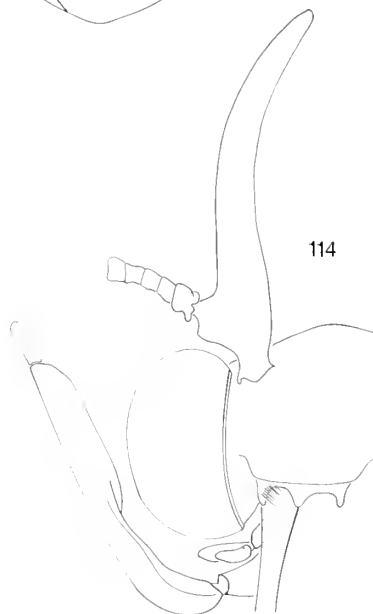
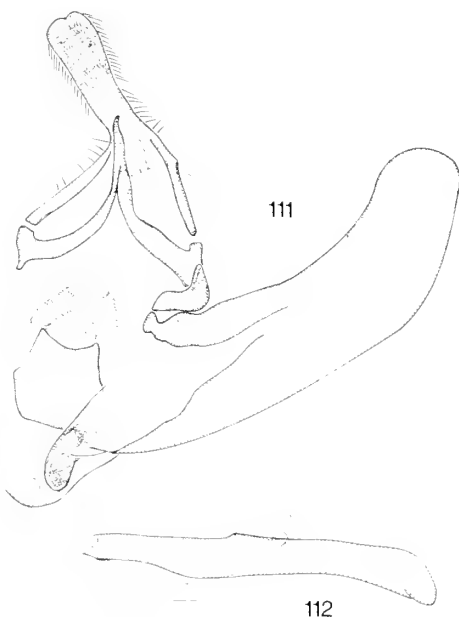
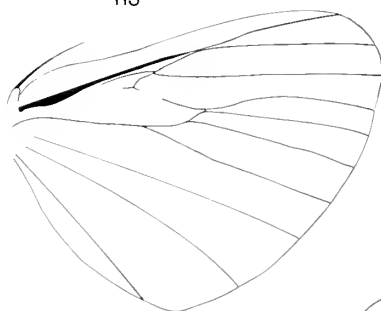
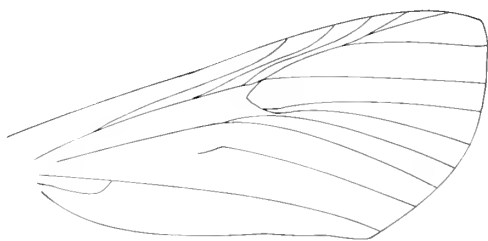
Characters. For the cladistic analysis of the *Pococera* complex 24 terminal taxa and 65 characters were used to develop a character matrix (Table 1). The characters were discussed in the Morphology section and are listed in the Morphology section.

In the following discussion and Figure 137, "autapomorphy" means a transformation to a derived condition only in a terminal taxon. At the interior nodes, a transformation to a derived condition occurring only once on the tree is termed a strong or unique synapomorphy. A "reversal" denotes a transformation to a plesiomorphic condition occurring only once on the tree. A "parallelism" denotes a synapomorphy of multiple origin or a multiple reversion to a primitive state either at a terminal taxon or a node.

Stability tests. Homoplasy (parallelisms, convergences, reversals), coupled with incomplete sampling of taxa, introduces error into tree estimation. A variety of approaches have been suggested for empirically gauging the stability or robustness of phylogeny estimates (Farris, 1969; Micevich, 1978; Felsenstein, 1985; Lanyon, 1985). These involve sub- or re-sampling (or re-weighting) of either the taxa or the characters. The trees produced by the Wagner analysis of the *Pococera* complex were subjected to two such kinds of tests, successive weighting and sequential removal of



Figs. 105–109. *Macalla thyrsisalis* Walker. 105. Female genitalia #757 MAS. 106. Wings #151 MAS. 107. Male genitalia #756 MAS. 108. Aedeagus #756 MAS. 109. Male head #151 MAS.



Figs. 110–114. *Lacalma* n. sp. 110. Female genitalia #316 MAS. 111. Male genitalia #315 MAS. 112. Aedeagus #315 MAS. 113. Wings #315 MAS. 114. Male head #315 MAS.



115



116



117



118



119



120



121



122

Figs. 115–122. 115. *Anarnatula sylea* (Druce), Wing length = 7 mm. 116. *Cacozelia basi-ochrealis* Grote, Wing length = 9 mm. 117. *Carthara albicosta* Walker, Wing length = 15 mm. 118. *Cecidipta excoecariae* Berg, Wing length = 17 mm. 119. *Chloropaschia thermalis* Hampson, Wing length = 10 mm. 120. *Deuterollyta conspicialis* Lederer, Wing length = 11 mm. 121. *Milgithea melanoleuca* (Hampson), Wing length = 8 mm. 122. *Oneida lunulalis* Hulst, Wing length = 10 mm.



123



124



125



126



127



128

Figs. 123–128. 123. *Phidotricha erigens* Ragonot, Wing length = 5 mm. 124. *Roeseliodes ochreosticta* Warren, Wing length = 11 mm. 125. *Tallula atrifascialis* Hulst, Wing length = 7 mm. 126. *Tancoa calitas* Druce, Wing length = 9 mm. 127. *Pococera militella* Zeller, Wing length = 10 mm. 128. *Toripalpus breviornatalis* Grote, Wing length = 10 mm.

taxa. Successive weighting (Farris, 1969) was applied to the data set to test the effect of homoplasy. It is an iterative, *a posteriori* procedure in which characters are weighted by their consistencies on each succeeding tree estimate until the tree does not change. This procedure should result in the emphasis of the best and most consistent set of characters (Farris, 1983; Carpenter, 1988), those that “fit a common branching pattern” (Farris, 1969). If the topology of the tree following successive weighting is different from the initial estimated tree, then the highly homoplasious characters may be introducing error into the analysis, decreasing confidence in the estimated tree.

As a second check on the stability of the tree, selected taxa basal to large clades,



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Figs. 129–135. 129. *Pandoflabella olivescens* (Schaus), Wing length = 10 mm. 130. *Bibasilaris trisulcata* (Warren), Wing length = 14 mm. 131. *Accinctapubes albifasciata* (Druce), Wing length = 12 mm. 132. *Mediavia discalis* (Hampson), Wing length = 9 mm. 133. *Quadraforma obliqualis* (Hampson), Wing length = 10 mm. 134. *Mazdacis consimilis* (Dognin), Wing length = 8 mm. 135. *Dasyvesica lophotalis* (Hampson), Wing length = 10 mm.

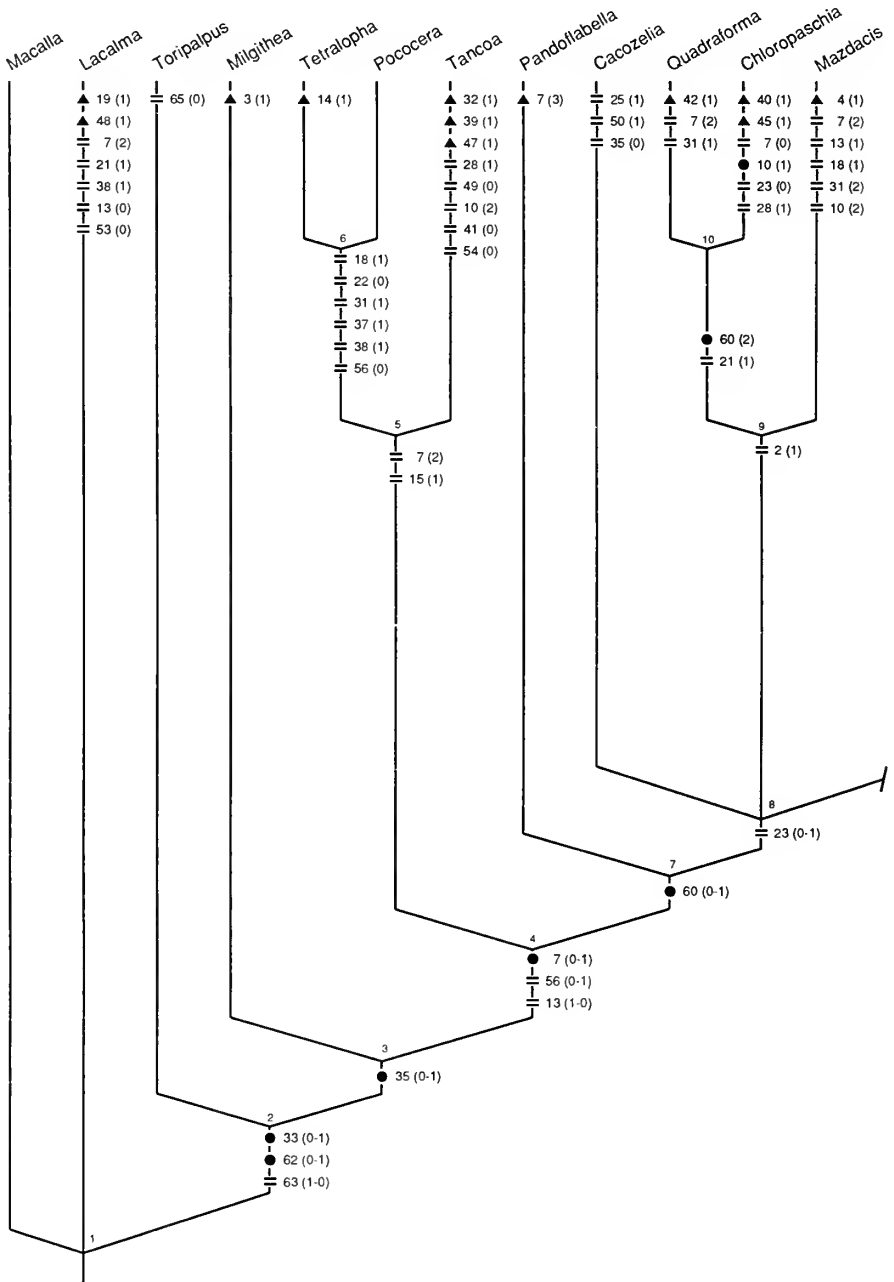
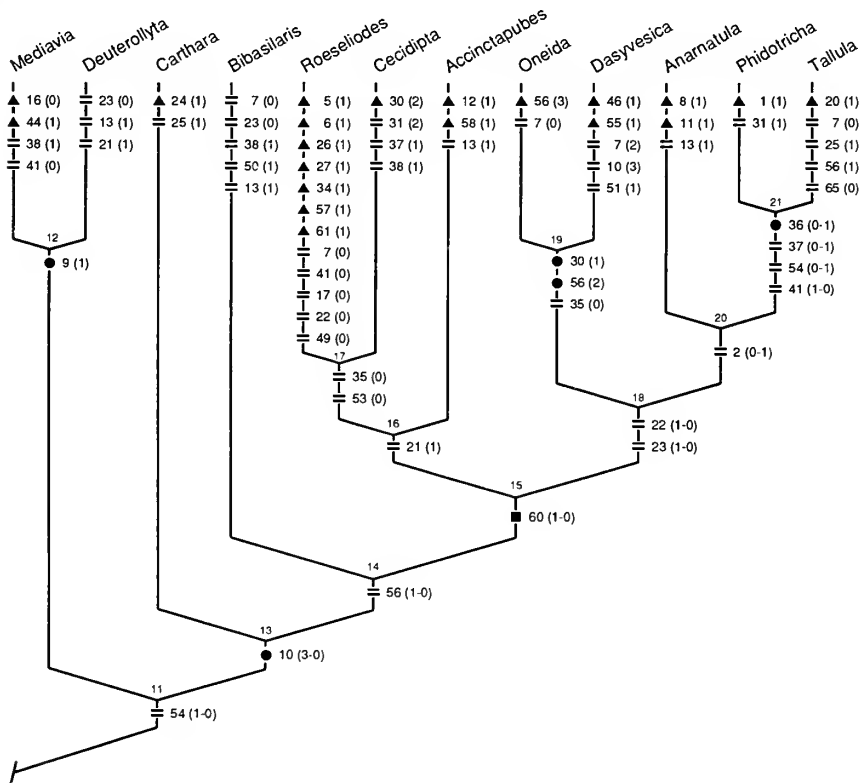


Fig. 136. One of three most equally parsimonious cladograms for the *Pococera* complex with *Macalla* and *Lacalma* as outgroups generated with the PHYSYS program. Numbers outside parentheses indicate character number, and those inside the parentheses indicate transformation states. All numbers correspond to those in the Summary of Character and States.



- ▲ autapomorphy
- synapomorphy
- parallelism
- reversal

Fig. 136. Continued.

especially clades defined only by homoplasious character(s), were removed one at a time from the data. The rationale is that, if the tree is being strongly influenced by homoplasious characters, changes in character distribution due to taxon sampling should strongly affect the estimate (Lanyon, 1985). The taxa removed were *Milgitha*, *Cacozelia*, *Pandoflabella*, *Bibasilaris*, *Accinctapubes*, *Toripalpus* and *Carthara*. Also, to test the effect of different outgroups, *Macalla* and *Lacalma* were removed sepa-

rately. This exercise allows the comparison of the stability of subsets within the *Pococera* complex when different outgroups are used. Subsets of taxa that remain the same after the removal of taxa are more stable than those that change.

Results. The phylogenetic analysis confirmed that there was considerable homoplasy in the data, but only three equally parsimonious trees were generated, of length 144 and consistency index 0.52. The disagreement among the three trees was the placement of two taxa, *Bibasilaris* and *Accinctapubes* (compare Figs. 137, 138). One tree was chosen for the purpose of discussion (Fig. 136). Successive weighting produced two trees with the same general topology as the tree chosen for discussion. Changes in the topology of the trees is discussed at the node in question. In the following discussion the characters are indicated by numbers in parentheses.

The analyses generally supported the monophyly of the *Pococera* complex. That is, the two outgroups, *Lacalma* and *Macalla*, came out together whenever they were both included (Farris, 1972), except when *Carthara* was removed. Removal of *Carthara*, with the tree rooted at *Macalla*, placed *Lacalma* inside the complex as a member of a clade including the *Pococera* clade (*Tetralopha* + *Pococera* + *Tancoa*) and the *Oneida* clade (*Oneida* + *Dasyvesica*) just above *Milgithea* and *Toripalpus* at the base of the tree. It seems unlikely that *Lacalma* lies inside the *Pococera* complex, since *Lacalma* lacks the two key synapomorphies of a prominent saccus and the narrow ductus bursae that diagnose the *Pococera* complex. This instability is attributable instead to the absence in the analysis of additional outgroups close to *Lacalma*.

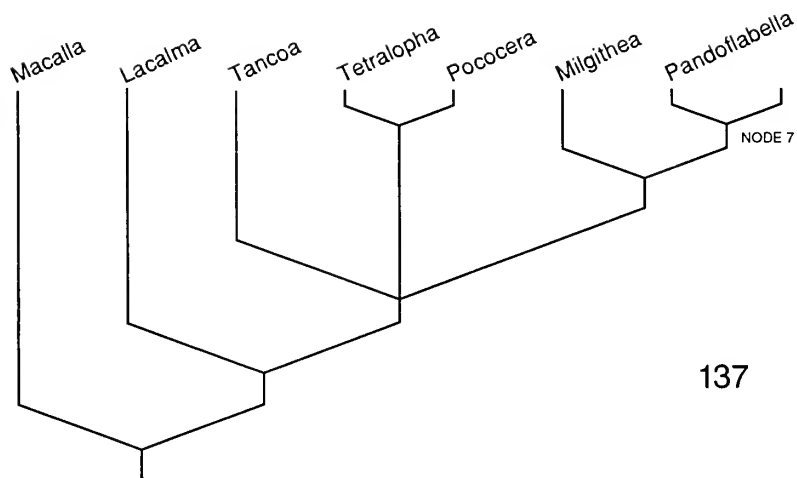
The estimate of the position of the root is somewhat unstable since the arrangement of the apparently basal elements, e.g., the *Pococera* clade, *Milgithea*, and *Toripalpus*, differs when only *Lacalma* is used as the outgroup or when *Toripalpus* is removed. In the analyses, node 3 and node 5 in effect exchange positions (Figs. 136, 139). This results from conflicting distributions of several character states in *Macalla*, and *Lacalma* and *Toripalpus*. The characters in question are the presence or absence of a frenulum hook and of a lobe at the base of the valva, and the width of the caudal end of the uncus. These characters are highly homoplasious on the tree. Nevertheless, the basal elements, the *Pococera* clade, *Milgithea*, and *Toripalpus*, are clearly identified.

Although the root is thus somewhat uncertain, many of the clades were maintained. All other manipulations did not destabilize the tree (Fig. 136) despite the fact that most groups are supported by very few characters. The only disagreement in almost all trees was the placement of *Bibasilaris* and *Accinctapubes*.

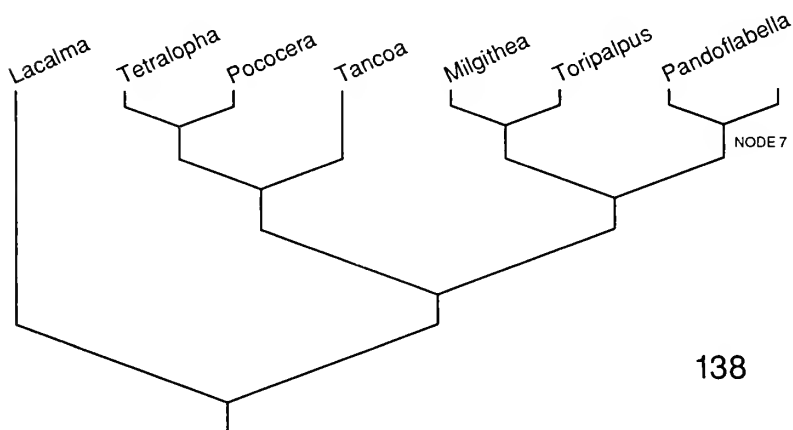
At node 3 *Milgithea* is the sister group to the remainder of the *Pococera* complex and is diagnosed by one homoplasious synapomorphy, the presence of the sclerotized structure at the base of the uncus (35). This state is lost several times in the remainder of the clade. The removal of *Milgithea* from the analysis did not destabilize the general topology of the tree.

Node 4 consists of the *Tancoa* + *Pococera* (*sensu lato*) clade and node 7. It is diagnosed by a unique synapomorphy and two homoplasious synapomorphies. The origin of a concave second labial segment (7) occurs only once on the tree. The two highly homoplasious states diagnosing this node are an absent frenulum hook (13) that re-appears in several taxa, and the presence of a long, pointed medial lobe in the juxta (56), which is subsequently lost and regained.

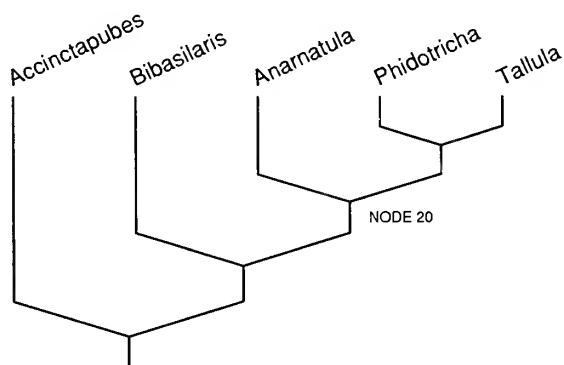
Node 5 is diagnosed by a unique combination of homoplasious characters. The



137



138



139

Figs. 137–139. 137, 138. Alternate placement of *Bibasilaris* and *Accinctapubes* upon different manipulations. 139. Alternate placement of *Pococera* clade, *Milgitea*, and *Toripalpus* upon successive weighting and sequential taxon removal.

second segment of the labial palpus is tubular (7), and R_1 and R_2 are fused in the forewing (15). The sister group relationship of *Pococera* and *Tetralopha* (node 6) is fairly well established. This group is diagnosed by a unique combination of six characters: a relatively short discocellular cell (18), a third anal vein (22) that is not coincident with the second anal vein, a tip of the tegumen sclerite as broad as the base (31), a single row of caudal setae on the uncus (37), a caudal end of the uncus wider than the width of the midpoint (38), and a juxta with a small, round medial lobe (56). *Pococera* was included to show that no synapomorphies were detected to define it. Therefore *Tetralopha* is synonymized under *Pococera* (see Morphology and Taxonomic Synopsis for further discussion).

Node 7 includes *Pandoflabella* as the basal taxon and is diagnosed by one unique synapomorphy in the female genitalia. The lamella antevaginalis (60) has a ventral fold that is entire or only weakly bilobed. The removal of this genus does not destabilize the topology of the tree.

Node 8 includes *Cacozelia*, node 9, and node 11, which form the only trichotomy in the tree. It is defined by a highly homoplasious separation of veins $Sc+R_1$ and R_s of the hindwing (23). Removal of *Cacozelia* does not destabilize the tree topology.

Node 9 includes *Chloropaschia*, *Quadraforma*, and *Mazdacis* and is diagnosed by the homoplasious reduction of the scape (2). The modified scape is lost again at node 20. The sister group relationship of *Quadraforma* and *Chloropaschia* (node 10), is defended by a unique synapomorphy in the female genitalia. The lamella antevaginalis (60) has a ventral fold that is strongly bilobed. It is also diagnosed by the homoplasious presence of a first anal vein in the forewing (21) that is gained several times.

Node 11 includes *Mediavia* + *Deuterollyta*, and node 13. It is diagnosed by the homoplasious reduction of the juxta arms (54). In almost all manipulations, the sister group relationship of node 12 and node 13 was maintained. The sister group relationship of *Mediavia* and *Deuterollyta* is based on a single unique synapomorphy: the base of the first segment of the maxillary palpus is membranous and pleated (9).

Node 13 includes *Carthara* plus node 14 and is diagnosed by a unique synapomorphy. The third segment of the maxillary palpus (10) is at the apex of the second segment. Removal of *Carthara* affects the placement of the group *Oneida* + *Dasyvesica* and of *Lacalma* (as discussed earlier), but does not otherwise change the tree. The transformation of state 3, the third segment of the maxillary palpus arising at the base of the second segment, to state 0, the third segment of the maxillary palpus arising at the apex of the segment, occurs only once on the tree, but the character is multistate and homoplasious. Degeneration of the character to less than four states would result in loss of information since states 1 and 2 are unique to terminal taxa. Alternatively, the character could prove to be too homoplasious to provide any consistent information on phylogeny. For example, the sister group relationship of *Oneida* and *Dasyvesica* is well defended by other characters and yet the states for the placement of the third maxillary segment in the two genera are at the two extremes of this four state transformation series. Further resolution by study of the maxillary palpus in the Pyralidae may solve the polarity problem of this character.

Node 14 includes *Bibasilaris* and node 15 and is also diagnosed by a homoplasy. The medial lobe of the juxta (56) is small and round. This node is not well defended, but removal of *Bibasilaris* causes little destabilization. In most analyses *Bibasilaris* was placed either as the sister group to node 15 (Fig. 136) or node 20 (Fig. 139). The placement of this genus is not resolved.

Node 15 consists of node 16 and node 18 and is diagnosed by a reversal. The lamella antevaginalis of the female genitalia (60) lacks a ventral fold. Despite the homoplasious character state, the clade is fairly stable, because all manipulations resulted in the inclusion of the same terminal taxa.

Node 16 consists of *Roeseliodes*, *Cecidipta* and *Accinctapubes* and is diagnosed by a highly homoplasious synapomorphy, loss of the first anal vein of the forewing (21). While removal of *Accinctapubes* does not destabilize the remainder of the tree, the placement of *Accinctapubes* is not well resolved. *Accinctapubes* was also placed as the sister group to a clade including *Bibasilaris* and node 20 (Fig. 139) when either *Carthara*, *Toripalpus* or *Pandoflabella* were removed and when only *Lacalma* was used as the outgroup. The sister group relationship of *Roeseliodes* and *Cecidipta* (node 17) is defended by two homoplasious characters: loss of the sclerotized structure at the base of the uncus (35), which occurs several times in the tree, and the loss of juxtal arms (53), which occurs also in *Lacalma*.

Node 18 is diagnosed by two homoplasious characters. The third anal vein (22) is not coincident with the second anal vein in the forewing and in the hindwing $Sc+R_1$ and Rs are fused (23). The relationship of node 19 and node 20 is not well defended. When *Toripalpus* is removed and *Lacalma* is used as an outgroup, node 19 is the sister group of node 17 and when *Carthara* is removed node 19 is placed in a clade at the base of the tree with the *Pococera* clade.

The sister group relationship of *Oneida* and *Dasyvesica* is well defended by two unique synapomorphies and one homoplasy. The tegumen sclerite (30) reaches a midventral position and the juxta (56) lacks lobes. The sclerotized structure at the base of the uncus (35) is lost several times on the tree.

Node 20, consisting of *Anarnatula*, *Phidotricha*, and *Tallula*, is defined by a parallelism, the loss of an elongate scape (2). Despite the parallelism, all manipulations resulted in the clustering of these three taxa.

The sister group relationship of *Phidotricha* and *Tallula* (node 21) is supported by a unique synapomorphy. The sclerotized structure at the base of the uncus (36) is triangular rather than U-shaped. Three homoplasies also diagnose this clade: the presence of a single caudal row of setae on the uncus (37), elongate juxtal arms (54) that extend to and beyond the costa of the valva, and the absence of a (41) medial lobe on the base of the valva.

Discussion. Two main problems are apparent with the results of the phylogenetic analysis. First, the relationships among the relatively primitive genera are unsettled, as exhibited by the instability on removal of some taxa, and the use of a different outgroup. Characters associated with these problems are highly homoplasious and warrant in-depth study across all taxa in the Epipaschiinae. Such a study would test the polarity and transformation series of the characters used in this study. The second problem, the placement of *Bibasilaris* and *Accinctapubes* is not resolved. Future placement of these genera may depend on discovery of additional characters.

Despite these problems, certain clades are stable, always clustering together despite the manipulation. This is evidenced by the general correspondence of the trees produced by the Wagner analysis and successive weighting. While there is much homoplasy, many characters on the trees are hierarchically correlated producing a stable tree. This estimated phylogeny will serve as a hypothesis to be tested further. Logically, two lines of systematic inquiry in the Epipaschiinae follow the present study. The genera of the *Pococera* complex should be revised at the species level. Second,

outgroups that have been studied in-depth at the species level should be added and used in cladistic analyses. Studies on the remaining genera outside the *Pococera* complex might resolve some of the questions about basal relationships and character evolution in the *Pococera* complex.

Inferences about biogeography based on this estimate of relationship of the *Pococera* complex are difficult primarily due to the overlap of distributions for almost all genera, and secondarily, to the lack of resolution at the species level and the paucity of collected material, hence a paucity of information on the entire range of the organisms.

Hypotheses of insect-plant relationships are speculative because of the paucity of corroborated information on host-plant associations in many of the genera. At first glance, the list of hosts utilized (Table 2) appears to be taxonomically disparate. But recent work has uncovered a host utilization pattern correlating many unrelated plant families which share a common defense syndrome: latex and resinous canals (Dussourd and Eisner, 1987; Farrell et al., 1991). Among the canal-bearing hosts in the *Pococera* complex are Sapotaceae, Fabaceae, Pinaceae, Anacardiaceae, Icacinaceae, Euphorbiaceae, and Moraceae. Departures from association with canal-bearing or resinous plants are species found on temperate plant groups and polyphages. For example, *Tancoa* is a specialist on canal-bearing plants and occurs from southern Mexico to Brazil and the occasionally polyphagous *Pococera* occurs from Brazil north to Canada. Some species of *Pococera* and *Phidotricha* appear to be oligophagous; in fact only one or two species are feeders on a wide variety of plant families. In *Pococera* many different species feed on resinous legumes, and one species feeds on Anacardiaceae, Fabaceae, Aceraceae, Ulmaceae, Fagaceae, Juglandaceae, and Carpinaceae. One species of *Tancoa* feeds on the laticiferous Icacinaceae, whereas the sister group of *Tancoa*, *Pococera*, has species feeding on resin-canal bearing Pinaceae or resinous legumes. If the ancestor of the two groups is hypothesized to feed on canal-bearing plants, this could have predated *Pococera* radiation into temperate areas. Genera associated with canal-bearing plants are *Milgithea*, *Pococera*, *Tancoa*, and *Cecidipta*. The first three genera, basal on the cladogram, could be hypothesized to be primitively associated with canal-bearing plants. A species of *Cecidipta* is associated with Euphorbiaceae and Moraceae, but few records exist between *Cecidipta* and the basal genera. As a result the association of *Cecidipta* with canal-bearing plants could be interpreted as being either plesiomorphic or a parallelism. Discovery of canal-bearing hosts for intermediary genera would support the hypothesis of plesiomorphy. The hypothesis of convergence seems less likely, *a priori*, because of certain complex behaviors generally associated with insects feeding on laticiferous plants (Dussourd and Eisner, 1987) that have been documented in *Cecidipta* and probably characterize cladistically basal genera likewise associated with canal-bearing plants. In at least one species of *Cecidipta*, eggs are laid on fly-induced galls on the stem and early instars feed on the gall. If there is not enough food in the gall for the development of the caterpillar, it exits the gall, severs leaf petioles, and returns to the gall with the leaves (Berg, 1877). The specialized behaviors allow the caterpillar to avoid latex defenses of the plant which it would no doubt encounter were it to feed directly on intact tissues. Similar behaviors have been documented for other lepidopteran associations with various laticiferous plants (Dussourd and Eisner, 1987). I expect that *Roeseliodes*, the highly derived sister group of *Cecidipta*, is probably also associated

with laticiferous plants and may exhibit specialized behaviors for countering latex defense.

Some of the similarities in host plant associations in the *Pococera* complex may be attributable to similarity in chemistry. Two distantly related plant families share benzylisoquinoline alkaloids, known to be toxic to most non-adapted herbivores (Miller and Feeny, 1983). Several genera (*Deuterollyta*, *Accinctapubes* and *Tallula*) have a majority of species known to feed on Lauraceae and Rutaceae. Thus, the apparent parallel associations with the families may reflect a common inherited ability to detoxify the noxious compounds.

NOMENCLATURAL SUMMARY

Accinctapubes Solis, new genus

albifasciata (Druce, 1902) (*Cecidiptera*), missp., N. COMB.

leucoplagialis (Hampson, 1906) (*Stericta*), N. SYN.

ban (Dyar, 1916) (*Jocara*), N. SYN.

anthimusalis (Schaus, 1925) (*Stericta*), N. COMB.

apicalis (Schaus, 1906) (*Jocara*), N. COMB.

elphegealis (Schaus, 1934) (*Cecidiptera*), N. SYN.

chionopheralis (Hampson, 1906) (*Stericta*), N. COMB.

Anarnatula Dyar, 1918

subflavida Dyar, 1918

sylea (Druce, 1899) (*Pycnulia*)

hyporhoda Dyar, 1918

Bibasilaris Solis, new genus

erythea (Druce, 1900) (*Homura*), N. COMB.

paranensis (Schaus, 1906) (*Macalla*)

ineldolis (Schaus, 1934) (*Macalla*), N. SYN.

trisulcata (Warren, 1891) (*Homura*), N. COMB.

viriditincta (Schaus, 1912) (*Locastra*)

Cacozelia Grote, 1877

albomedialis (Barnes & Benjamin, 1924) (*Epipaschia*), N. COMB.

pemphusalis (Druce, 1899) (*Pococera*), N. SYN.

basiochrealis Grote, 1877

elegans (Schaus, 1912) (*Pococera*), N. COMB.

neotropica (Amsel, 1956) (*Tioga*?), N. SYN.

interruptella (Ragonot, 1888) (*Epipaschia*), N. COMB.

dentilineella (Hulst, 1900) (*Jocara*)

Carthara Walker, 1865

Leptosphetta Butler, 1878, N. SYN.

Pycnulia Zeller, 1881, N. SYN.

abrupta (Zeller, 1881) (*Pycnulia*), N. COMB.

albicosta Walker, 1865

scopipes (Felder & Rogenhofer, 1875) (*Idia*), N. SYN.

rabdina (Butler, 1878) (*Leptosphetta*), N. SYN.

ministra (Zeller, 1881) (*Pycnulia*), N. SYN.

Cecidiptera Berg, 1877

Accecidiptera Amsel, 1956, N. SYN.

- cecidiptoides* (Schaus, 1925) (*Stericta*), N. COMB.
excoecariae Berg, 1877
 phyalis (Druce, 1899) (*Locastra*)
 abnormalis Dognin, 1904, N. SYN.
 albescens (Schaus, 1906) (*Macalla*)
 olivencia (Schaus, 1906) (*Jocara*), N. SYN.
 mirosema (Meyrick, 1936) (*Earoctenis*), N. SYN.
 major (Amsel, 1956) (*Acecidipta*), N. COMB.
 teffealis (Schaus, 1922) (*Stericta*), N. COMB.
Chloropaschia Hampson, 1906
 adesia Schaus, 1925
 afflicta (Schaus, 1922) (*Macalla*)
 aniana Schaus, 1925
 brithvalda Schaus, 1922
 canities Schaus, 1912
 contortilinealis (Dognin, 1908) (*Stericta*), N. COMB.
 rufilinea (Druce, 1910) (*Macalla*)
 epipodia Schaus, 1925
 fabianalis Schaus, 1922
 fiachnalis Schaus, 1925
 godrica Schaus, 1934
 granitalis (Felder & Rogenhofer, 1875) (*Homura*?)
 hemileuca (Dognin, 1910) (*Stericta*), N. COMB.
 hollandalis Schaus, 1925
 lascertianalis Schaus, 1934
 lativalva (Amsel, 1956) (*Arnatula*?), N. COMB.
 mennusalis Schaus, 1922
 nadena Schaus, 1934
 pegalis (Schaus, 1922) (*Macalla*), N. COMB.
 possidia (Schaus, 1925) (*Stericta*), N. COMB.
 rufibasis (Druce, 1910) (*Macalla*), N. COMB.
 claphealis (Schaus, 1912) (*Macalla*), N. SYN.
 brunnapex (Kaye, 1922) (*Pococera*), N. SYN.
 selecta (Schaus, 1912) (*Macalla*), N. COMB.
 thermalis Hampson, 1906
 venantia Schaus, 1925
Dasyvesica Solis, 1991
 lophotalis (Hampson, 1906) (*Jocara*)
 nepomuca (Schaus, 1925) (*Pococera*)
 crinitalis (Schaus, 1922) (*Jocara*)
Deuterollyta Lederer, 1863
 Winona Hulst, 1888, N. SYN.
 Oedomia Dognin, 1906, N. SYN.
 Ajocara Schaus, 1925, N. SYN.
 Ajacania Schaus, 1925, N. SYN.
 abachuma (Schaus, 1922) (*Jocara*), N. COMB.
 acheola (Schaus, 1925) (*Jocara*), N. COMB.

- aidana* (Schaus, 1922) (*Jocara*), N. COMB.
agathoa (Schaus, 1922) (*Jocara*), N. COMB.
albiferalis (Hampson, 1916) (*Jocara*), N. COMB.
albimedialis (Hampson, 1916) (*Jocara*), N. COMB.
amazonalis (Schaus, 1925) (*Jocara*), N. COMB.
anacita (Schaus, 1925) (*Jocara*), N. COMB.
anastasia (Schaus, 1922) (*Jocara*), N. COMB.
andeola (Schaus, 1925) (*Jocara*), N. COMB.
ansberti (Schaus, 1922) (*Jocara*), N. COMB.
anathasia (Schaus, 1925) (*Jocara*), N. COMB.
basilata (Schaus, 1912) (*Isolopha*), N. COMB.
bryoxantha (Meyrick, 1936) (*Jocara*), N. COMB.
cacalis (Felder & Rogenhofer, 1875) (*Hemimattia?*), N. COMB.
cantianilla (Schaus, 1925) (*Jocara*), N. COMB.
chrysoderas (Dyar, 1917) (*Pococera*), N. COMB.
chlorisalis (Schaus, 1912) (*Jocara*), N. COMB.
claudalis (Moeschler, 1866) (*Hemimattia*), N. COMB.
cononalis (Schaus, 1922) (*Jocara*), N. COMB.
conrana (Schaus, 1922) (*Jocara*), N. COMB.
conspicualis Lederer, 1863
 medusa (Druce, 1902) (*Stericta*), N. SYN.
cristalis Felder & Rogenhofer, 1875
dapha (Druce, 1895) (*Jocara*), N. COMB.
desideria (Schaus, 1925) (*Jocara*), N. COMB.
extensa (Walker, 1863) (*Nephopteryx*), N. COMB.
 variegata Warren, 1891
francesca Jones, 1912
 egvina (Schaus, 1922) (*Tallula*), N. SYN.
fusculifusalis (Hampson, 1916) (*Pococera*), N. COMB.
 theodota (Schaus, 1925) (*Jocara*), N. SYN.
hemizonalis (Hampson, 1916) (*Jocara*), N. COMB.
hispida (Dognin, 1906) (*Oedomia*), N. COMB.
 amazona (Schaus, 1925) (*Ajocara*), N. SYN.
hospitia (Schaus, 1925) (*Jocara*), N. COMB.
lactiferalis (Hampson, 1916) (*Jocara*), N. COMB.
lutosalis (Amsel, 1956) (*Jocara*), N. COMB.
majuscula Herrich-Schaeffer, 1871
 incrustalis (Hulst, 1887) (*Toripalpus*), N. SYN.
 infectalis Moeschler, 1890
 ferriusalis (Hampson, 1906) (*Jocara*), N. SYN.
 obscuralis (Schaus, 1912) (*Jocara*), N. SYN.
 perseella (Barnes & McDunnough, 1913) (*Jocara*), REV. STAT.
 musettalis (Schaus, 1934) (*Jocara*), N. SYN.
malrubia (Schaus, 1934) (*Cecidipta*), N. COMB.
maroa (Schaus, 1922) (*Jocara*), N. COMB.
martinia (Schaus, 1922) (*Jocara*), N. COMB.
maurontia (Schaus, 1925) (*Jocara*), N. COMB.

- mava* (Schaus, 1925) (*Jocara*), N. COMB.
mediosinialis (Hampson, 1916) (*Pococera*), N. COMB.
monosemia (Zeller, 1881) (*Myelois*), N. COMB.
multicolor (Dognin, 1904) (*Stericta*), N. COMB.
nigripuncta (Schaus, 1912) (*Jocara*), N. COMB.
oduvalda (Schaus, 1925) (*Jocara*), N. COMB.
oediperalis (Hampson, 1906) (*Jocara*), N. COMB.
phileasalis (Schaus, 1925) (*Ajocara*), N. SYN.
pagiroa Schaus, 1906
prudentia (Schaus, 1925) (*Jocara*), N. COMB.
pyropicta (Schaus, 1934) (*Jocara*), N. COMB.
ragonoti Moeschler, 1890
raymonda (Schaus, 1922) (*Jocara*), N. COMB.
rufitinctalis (Hampson, 1906) (*Tetralopha*), N. COMB.
sara (Schaus, 1925) (*Jocara*), N. COMB.
sisinnia (Schaus, 1925) (*Jocara*), N. COMB.
subcurvalis (Schaus, 1912) (*Jocara*), N. COMB.
subfusca (Schaus, 1912) (*Jocara*), N. COMB.
suiferens (Dyar, 1913) (*Jocara*), N. COMB.
tenebrosa (Schaus, 1912) (*Jocara*), N. COMB.
terrenalis (Schaus, 1912) (*Jocara*), N. COMB.
thermochroalis (Hampson, 1916) (*Jocara*), N. COMB.
translinea (Schaus, 1912) (*Jocara*), N. COMB.
umbrosalis (Schaus, 1912) (*Jocara*), N. COMB.
yva (Schaus, 1925) (*Jocara*), N. COMB.
steinbachalis (Schaus, 1925) (*Ajacania*), N. SYN.
zetila (Druce, 1902) (*Stericta*), N. COMB.
luciana (Schaus, 1922) (*Jocara*), N. SYN.

Mazdacis Solis, new genus

- consimilis* (Dognin, 1911) (*Epipaschia*), N. COMB.
flavomarginata (Druce, 1902) (*Stericta*), N. COMB.
soteris (Schaus, 1922) (*Auradisa*), N. SYN.
zenoa (Schaus, 1925) (*Chloropaschia*), N. COMB.

Mediavia Solis, new genus

- aciusa* (Schaus, 1925) (*Macalla*), N. COMB.
agnesa (Schaus, 1922) (*Tetralopha*), N. COMB.
bevnoa (Schaus, 1925) (*Stericta*), N. COMB.
discalis (Hampson, 1906) (*Jocara*), N. COMB.
dissimilis (Warren, 1891) (*Roeseliodes*), N. COMB.
eadberti (Schaus, 1925) (*Stericta*), N. COMB.
emerantia (Schaus, 1922) (*Stericta*), N. COMB.
glaucinalis (Hampson, 1906) (*Stericta*), N. COMB.
paschasia (Schaus, 1925) (*Stericta*), N. SYN.
grenvilalis (Schaus, 1934) (*Jocara*), N. COMB.
hermengilda (Schaus, 1925) (*Stericta*), N. COMB.
ildefonsa (Schaus, 1922) (*Stericta*), N. COMB.
internigralis (Dognin, 1909) (*Pococera*), N. COMB.

longistriga (Schaus, 1922) (*Jocara*), **N. COMB.**

comgalla (Schaus, 1925) (*Stericta*), **N. SYN.**

phaebadia (Schaus, 1925) (*Stericta*), **N. COMB.**

vimina (Schaus, 1922) (*Jocara*), **N. COMB.**

Milgithea Schaus, 1922

albhoplialialis (Dyar, 1904) (*Cacozelia*), **N. COMB.**

melanoleuca (Hampson, 1896) (*Pococera*)

rufiapicalis (Hampson, 1916) (*Jocara*)

suramisa Schaus, 1922

trilinearis (Hampson, 1906) (*Jocara*)

Oneida Hulst, 1889

grisiella Solis, 1991

lunulalis Hulst, 1888

luniferella Hulst, 1895

marmorata (Schaus, 1913) (*Pococera*)

mejona Schaus, 1922

diploa Dyar, 1920

***Pandoflabella* Solis, new genus**

brendana (Schaus, 1925) (*Auradisa*), **N. COMB.**

corumbina (Schaus, 1925) (*Auradisa*), **N. COMB.**

fechina (Schaus, 1922) (*Auradisa*), **N. COMB.**

guianica (Schaus, 1925) (*Auradisa*), **N. COMB.**

nigrilunalis (Dognin, 1913) (*Pococera*), **N. COMB.**

nigriplaga (Dognin, 1910) (*Auradisa*), **N. COMB.**

olivescens (Schaus, 1912) (*Pococera*), **N. COMB.**

remberta (Schaus, 1922) (*Auradisa*), **N. COMB.**

stenipteralis (Hampson, 1906) (*Pococera*), **N. COMB.**

strigidiscalis (Hampson, 1916) (*Auradisa*), **N. COMB.**

tresaina (Schaus, 1922) (*Auradisa*), **N. COMB.**

Phidotricha Ragonot, 1888

Eutrichocera Hampson, 1904, **N. SYN.**

Jocarula Dyar, 1925, **N. SYN.**

agriperda (Dyar, 1925) (*Jocarula*), **N. COMB.**

baradata (Schaus, 1922) (*Pococera*)

erigens Ragonot, 1888

dryospila (Meyrick, 1936) (*Auradisa*), **N. SYN.**

insularella (Ragonot, 1888) (*Tetralopha*), **N. COMB.**

paurolepidalis (Hampson, 1904) (*Eutrichocera*), **N. SYN.**

limalis (Schaus, 1922) (*Pococera*)

vedastella (Schaus, 1922) (*Pococera*)

Pococera Zeller, 1848

Tetralopha Zeller, 1848, **REV. SYN.**

Lanthaphe Clemens, 1860, **REV. SYN.**

Hemimatia Lederer, 1863, **REV. SYN.**

Benta Walker, 1863, **REV. SYN.**

Auradisa Walker [1866] 1865, **REV. SYN.**

Saluda Hulst, 1888, **REV. SYN.**

- Katona* Hulst, 1888, **REV. SYN.**
Loma Hulst, 1888, **REV. SYN.**
Wanda Hulst, 1888, **REV. SYN.**
Tioga Hulst, 1888, **N. SYN.**
Attacapa Hulst, 1889, **REV. SYN.**
aelfredella (Schaus, 1922) (*Tetralopha*), **REV. COMB.**
albiceps Hampson, 1906
antilocho (Meyrick, 1936) (*Oneida*), **N. COMB.**
aplastella (Hulst, 1889) (*Tioga*), **N. COMB.**
arizonella (Barnes & Benjamin, 1924) (*Tetralopha*), **N. COMB.**
asperatella (Clemens, 1860) (*Lanthape*), **REV. COMB.**
baptisiella (Fernald, 1871) (*Tetralopha*), **N. COMB.**
basalis (Jones, 1912) (*Stericta*), **N. COMB.**
 notabilis (Schaus, 1912) (*Pococera*), **N. SYN.**
basilissa (Schaus, 1922) (*Tetralopha*), **N. COMB.**
callipeplella (Hulst, 1888) (*Tetralopha*), **N. COMB.**
cataldusa (Schaus, 1925) (*Tetralopha*), **N. COMB.**
cuthmana (Schaus, 1922) (*Tetralopha*), **N. COMB.**
dolorosella (Barnes & Benjamin, 1924) (*Tetralopha*), **N. COMB.**
euphemella (Hulst, 1888) (*Katona*), **N. COMB.**
 variella Ragonot, 1888
 melanographella Ragonot, 1888
expandens (Walker, 1863) (*Benta*), **REV. COMB.**
 nephelotella (Hulst, 1888) (*Loma*), **N. COMB.**
 clemensalis (Dyar, 1904) (*Tetralopha*), **N. COMB.**
floridella (Hulst, 1900) (*Benta*), **N. COMB.**
fuscolotella (Ragonot, 1888) (*Tetralopha*), **REV. COMB.**
gelidalis (Walker, [1866] 1865) (*Auradisa*), **REV. COMB.**
 subalbella (Walker, 1866) (*Myelois*), **REV. COMB.**
 tertiella Dyar, 1905, **N. SYN.**
 irrorata Schaus, 1912, **N. SYN.**
gibbella Zeller, 1848
griscella (Barnes & Benjamin, 1924) (*Tetralopha*), **N. COMB.**
gybriana (Schaus, 1925) (*Tetralopha*), **N. COMB.**
hemimelas Hampson, 1906
 basigera Dyar, 1914
 vanenga (Schaus, 1922) (*Tetralopha*), **N. SYN.**
hermasalis (Schaus, 1925) (*Tetralopha*), **N. COMB.**
humarella (Ragonot, 1888) (*Tetralopha*), **REV. COMB.**
 formosella (Hulst, 1900) (*Tetralopha*), **N. COMB.**
iogalis (Schaus, 1922) (*Tetralopha*), **N. COMB.**
jovita (Schaus, 1922) (*Tetralopha*), **N. COMB.**
maritimalis (McDunnough, 1939) (*Tetralopha*), **N. COMB.**
melanogrammos (Zeller, 1872) (*Tetralopha*), **REV. COMB.**
militella (Zeller, 1848) (*Tetralopha*), **REV. COMB.**
 platanella (Clemens, 1860) (*Lanthape*)
nigribasalis Hampson, 1906

- polialis* Hampson, 1906
provoella (Barnes & Benjamin, 1924) (*Tetralopha*), N. COMB.
robustella Zeller, 1848
 diluculella (Grote, 1880) (*Tetralopha*)
sabbasa (Schaus, 1922) (*Tetralopha*), N. COMB.
scabridella (Ragonot, 1888) (*Tetralopha*), REV. COMB.
scortealis (Lederer, 1863) (*Hemimantia*), REV. COMB.
 slossi (Hulst, 1895) (*Benta*)
spaldingella (Barnes & Benjamin, 1924) (*Tetralopha*), N. COMB.
speciosella (Hulst, 1900) (*Benta*), N. COMB.
subcanalis (Walker, 1863) (*Nephopteryx*), REV. COMB.
 taleolalis (Hulst, 1886) (*Toripalpus*)
 querciella (Barnes & McDunnough, 1913) (*Tetralopha*)
texanella Ragonot, 1888
thoracicella (Barnes & Benjamin, 1924) (*Tetralopha*)
tiltella (Hulst, 1888) (*Wanda*), N. COMB.
vaciniivora (Munroe, 1963) (*Tetralopha*), N. COMB.
vandella Dyar, 1914
- Quadraforma** Solis, new genus
 maroniensis (Hampson, 1916) (*Stericta*), N. COMB.
 lamonti (Schaus, 1922) (*Pococera*), N. SYN.
 mianalis (Felder & Rogenhofer, 1875) (*Homura*?), N. COMB.
 obliquialis (Hampson, 1906) (*Stericta*), N. COMB.
 seminigralis (Hampson, 1916) (*Pococera*), N. COMB.
- Roeseliodes* Warren, 1891
 celsusalis (Schaus, 1934) (*Chloropaschia*), N. COMB.
 goanta (Schaus, 1922) (*Tancoa*), N. COMB.
 goantoides (Amsel, 1956) (*Arocopaschia*), N. COMB.
 ochreosticta Warren, 1891
 petamona (Schaus, 1925) (*Stericta*), N. COMB.
 pontealis (Schaus, 1925) (*Stericta*), N. COMB.
- Tallula* Hulst, 1888
 atramentalis (Lederer, 1863) (*Hemimantia*), N. COMB.
 atrifascialis (Hulst, 1886) (*Tetralopha*)
 baboquivarialis Barnes & Benjamin, 1926
 beroella (Schaus, 1912) (*Pococera*), N. COMB.
 bunniotis (Dyar, 1913) (*Tioga*), N. SYN.
 fieldi Barnes & McDunnough, 1913
 fovealis Hampson, 1906
 juanalisis Schaus, 1925
 melazonalis Hampson, 1906
 rigualis (Lederer, 1863) (*Hemimantia*), N. COMB.
 tersilla Dyar, 1914
 watsoni Barnes & McDunnough, 1917
- Tancoa* Schaus, 1922
 arciferalis (Hampson, 1916) (*Tetralopha*), N. COMB.
 attenualis (Hampson, 1906) (*Macalla*)

calitas (Druce, 1899) (*Deuterollyta*)
sphaerophora (Dyar, 1914) (*Pococera*)
crinita (Schaus, 1912) (*Pococera*)
erlupha Schaus, 1922
metaxanthalis (Hampson, 1916) (*Pococera*)
pallidifusa (Dognin, 1913) (*Pococera*), **N. COMB.**
quiriguana Schaus, 1922, **N. SYN.**
sinuata Janse, 1931, **N. SYN.**
schausi Janse, 1931
silavia Schaus, 1925
ubalda Schaus, 1925
Toripalpus Grote, 1878
breviornatalis Grote, 1878
trabalis Grote, 1881

Incertae sedis.

admotalis (Dognin, 1904) (*Macalla*)
termenipuncta (Schaus, 1925) (*Macalla*)
albimedialis (Hampson, 1906) (*Pococera*)
albimedium (Schaus, 1912) (*Pococera*), **N. SYN.**
albulella (Hampson, 1896) (*Pococera*)
alnotha (Schaus, 1922) (*Stericta*)
atristrigella (Ragonot, 1893) (*Myelois*)
boliviana (Schaus, 1925) (*Macalla*)
canutusa (Schaus, 1922) (*Stericta*)
capnodon (Dyar, 1916) (*Pococera*)
circumlucens (Dyar, 1914) (*Arnatula*)
corumba (Schaus, 1922) (*Jocara*)
cyrilla (Schaus, 1922) (*Tetralopha*)
gillalis (Schaus, 1925) (*Jocara*)
glastianalis (Schaus, 1922) (*Macalla*)
grisealis (Hampson, 1906) (*Macalla*)
maidoa (Schaus, 1922) (*Stericta*)
marchiana (Schaus, 1922) (*Jocara*)
marginata (Schaus, 1912) (*Macalla*)
modana (Schaus, 1922) (*Lepidogma*)
nana (Schaus, 1912) (*Jocara*)
narthusa (Schaus, 1913) (*Pococera*)
neotropica (Amsel, 1956) (*Tioga*?)
nigrisquama (Dognin, 1904) (*Stericta*)
nigropunctata (Druce, 1902) (*Stericta*)
nolasca (Schaus, 1922) (*Stericta*)
noloides (Hampson, 1916) (*Jocara*)
olivescens (Druce, 1902) (*Stericta*)
albulatalis (Dognin, 1904) (*Macalla*), **N. SYN.**
palmistalis (Kaye, 1924) (*Stericta*)
parallelalis (Hampson, 1916) (*Jocara*)
pictalis (Hampson, 1906) (*Jocara*)

- rebeli* (Hedemann, 1896) (*Homara*)
rubralis (Hampson, 1916) (*Jocara*)
sadotha (Schaus, 1922) (*Wanda*?)
subviolascens (Hampson, 1906) (*Pococera*)
theliana (Schaus, 1922) (*Jocara*)
thilloa (Schaus, 1922) (*Jocara*)
venezuelensis (Amsel, 1956) (*Jocara*?)
violescens (Dyar, 1914) (*Lepidogma*)
viridis (Druce, 1910) (*Macalla*)
Anaeglis Lederer, 1863
demissalis Lederer, 1863
Apocera Schaus, 1912
Paranatula Dyar, 1913
colorata (Dyar, 1914) (*Arnatula*) [sic]
costata Schaus, 1912
vincentia Schaus, 1922
zographica (Dyar, 1922) (*Paranatula*)
Calybitia Schaus, 1922
adolescens (Dyar, 1914) (*Jocara*)
picata (Schaus, 1922) (*Calybitia*)
Geropaschia Hampson, 1917, replacement name
grisealis (Hampson, 1916) (*Araeopaschia*)
Homura Lederer, 1863
nocturnalis (Lederer, 1863) (*Homura*)
Incharca Dyar, 1910
aporalis (Dyar, 1910) (*Incarcha*)
argentilinea (Druce, 1910) (*Macalla*)
Isolopha Hampson, 1895
lactealis Hampson, 1895
Jocara Walker, 1863
fragilis Walker, 1863
Micropaschia Hampson, 1906
orthogrammalis Hampson, 1906
Nouanda Holland & Schaus, 1925
agatha (Schaus, 1922) (*Wanda*)
nocturna (Schaus, 1922) (*Wanda*)
Oxyalcia Dognin, 1905
mira (Druce, 1902) (*Macalla*)
ovifera (Dognin, 1905) (*Oxyalcia*)
Tineopaschia Hampson, 1916
minuta Hampson, 1916
Taxa removed from the Epipaschiinae.
Glossopaschia Dyar, 1914 to **Phycitinae**
caenoses Dyar, 1914
Pocopaschia Dyar, 1914 to **Galleriinae**
accelerans Dyar, 1914
brachypalpia (Dognin, 1910) (*Pococera*), N. COMB.

- bellangula* Dyar, 1914
noctuina (Schaus, 1912) (*Jocara*)
Proropoca Hampson, 1916 to **Galleriinae**
rubrescens Hampson, 1916
Stenopaschia Hampson, 1906 to **Galleriinae**
Stenopaschia Dyar, 1914, **PREOCC.**
Tapinolopha Dyar, 1918, **N. SYN.**
erythralis Hampson, 1906
gallerialis Hampson, 1916
epipaschiella (Hampson, 1917) (*Epimorius*), **N. SYN.**
trichopteris Dyar, 1914
variegata (Dyar, 1918) (*Tapinolopha*), **N. SYN.**
Xenophasma Dognin, 1905 to **Galleriinae**
notodontoides Dognin, 1905 to **Galleriinae**
chalcoclora Hampson, 1966 to **Pyraustinae**, *Mimudea* Warren
Genopaschia Dyar, 1914 to **Galleriinae**
protomis Dyar, 1914
irenealis (Schaus, 1940) (*Pseudotracha*), **N. SYN.**
Jocara lichfoldi Kaye to **Chrysauginae**, *Bonchis* Walker

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NEW JUNIOR SYNONYMS OF
FRANKLINIELLA RETICULATA AND *F. SIMPLEX*
(THYSANOPTERA: THRIPIDAE)

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Abstract.—*Frankliniella brunnea* Priesner, *F. fuscipennis* Moulton, *F. inopinata* Moulton, and *F. tridacana* Hood are junior synonyms of *F. reticulata* (Crawford), **NEW SYNONYMY**. The lectotype of *F. adadusta* Moulton is a junior synonym of *F. simplex* Priesner, **NEW SYNONYMY**, and the paralectotype is a different species, *F. reticulata*.

In a review of the junior synonyms of *Frankliniella cephalica* (Crawford) treated by Jacot-Guillarmod (1974:767), *Euthrips cephalica* var. *reticulata* Crawford (1910:155) was revalidated as a species in *Frankliniella* (Nakahara, 1992:415). The lectotype of *F. reticulata* was collected from Guadalajara, Mexico. Because of its close resemblance to *F. fuscipennis* Moulton (1948:105), the lectotype was compared with the holotype of *F. fuscipennis* from Guatemala and seven paratypes from Mexico. Although the measurements of several morphological characters of *F. fuscipennis* are generally greater than those of *F. reticulata* (Table 1), I conclude that *F. fuscipennis* is a junior synonym of *F. reticulata*, **NEW SYNONYMY**. Moulton (1948:105) states that the posteromarginal comb on abdominal tergite VIII of *F. fuscipennis* is absent medially. The comb of the holotype lacks microtrichia medially, but the paratypes have complete combs of short, sparse microtrichia. Those of the holotype apparently were broken off.

The holotype of *F. brunnea* Priesner (1932:174) from Mexico examined in this study has several morphological characters longer than the lectotype of *F. reticulata* and type series of *F. fuscipennis* (Table 1). However, the pedicel of antennal segment III, position of interocellar setae, posteromarginal comb on abdominal tergite VIII and general coloration are similar; I therefore consider *F. brunnea* to be a large specimen of *F. reticulata*, **NEW SYNONYMY**.

The type series of *Frankliniella tridacana* Hood (1937:104) from Panama is similar in color to the types of *F. fuscipennis* (= *F. reticulata*). Although measurements of several characters are shorter (Table 1), other characters of the females and males are similar. Thus, I consider *F. tridacana* to be a smaller form of *F. reticulata*, **NEW SYNONYMY**.

According to Moulton (1948:107), *Frankliniella inopinata* was described from a female and male taken in flowers of *Lantana* sp. at Cuernavaca, Mexico, by K. L. Krauss. The allotype slide has the aforementioned collection data and is labeled "*Frankliniella inopina* Mlt" with "*ta*" added in pencil. The holotype slide is labeled "*Frankliniella inopinus* Moulton" with the following collection data: Hidalgo, Texas 2152, 37-7448, Mexico, cutflowers, III-13-37, A. L. Williams. A card with the holotype slide contains the same measurements given in the description, and therefore,

Table 1. Measurements of types.

	<i>reticulata</i> (1)	<i>brunnea</i> (1)	<i>fuscipennis</i> (8)	<i>tridacana</i> (6)
Body length	1.33	1.5	1.37–1.55	1.27–1.52
AIII	47	57–59	49–54	43–49
IO setae	49	69	49–62	47–49
AM setae		64	47–64	40–52
PAI setae	74	94	67–91	54–72
PAO setae	62	86	62–79	56–62
B1 setae on IX	106	133	106–143	101–119

() = number of type specimens measured; AIII = antennal segment III; IO = interocellar; AM = anteromarginal; PAI = posteroangular inner; PAO = posteroangular outer; B1 = median pair. Measurements are in microns except for body length which is in millimeters.

I consider it to be the holotype of *F. inopinata*. Moulton apparently forgot to change the name to *inopinata* on the slide and correct the collection data in his description. In my opinion the holotype of *F. inopinata* is a smaller specimen of *F. reticulata*, NEW SYNONYMY. In compariaon with *F. reticulata*, the body is about 1.23 mm long and is lighter brown, forewings are pale with grayish brown tinge, and the measurements of the antennal segment III and setae fall in the variation given for *F. tridacana*. However, the pedicel of antennal segment III, position of interocellar setae, number of minor setae between the anteromarginal setae on the pronotum, and the posteromarginal comb are similar. The allotype is similar morphologically to males of *F. reticulata*, based on *F. fuscipennis*, but is light yellowish brown and probably is a teneral specimen.

Frankliniella reticulata is uniformly brown with orange internal pigmentation; the tarsi are yellowish brown to yellow, foretarsi are yellow, yellowish brown, or yellowish brown with margins brown, mid- and hindtibiae are completely brown to yellowish brown or yellow; ocellar crescent is red; forewings are completely brown; antennae are brown, except the pedicel of III is pale and basal one-half of III is yellowish brown, basal part of IV is pale or yellowish brown, and the short pedicel of V is brown with a pale ring just distal to it or the base of V is yellowish brown. The pedicel of antennal segment III has a small but distinct dilation, which is either rounded or angulate. The interocellar setae are positioned about midway between the anterior and posterior ocelli or are slightly closer to posterior ocelli. Two minor setae are between the anteromarginal setae on the pronotum. The forewings of 17–23 venal setae on the fore vein and 13–16 venal setae on the hind vein. Abdominal tergite VIII has a complete posteromarginal comb with short and sparse microtrichia and B1 setae on tergite IX are distinctly longer than segment X. The males are smaller, but similar in color and in most morphological characters to that of the females. Abdominal sternites III–VII each have a transversely elongate, elliptical glandular area.

Sculpturing on the lectotype of *F. reticulata* is not strongly reticulated as implied by the specific name.

Frankliniella reticulata is known from Mexico, Guatemala, Honduras, Costa Rica, Panama, Venezuela and Virgin Islands. It is commonly found on marigolds (*Tagetes*

spp.). Other recorded hosts are *Agapanthus* sp., *Chrysanthemum* sp., *Dianthus caryophyllus* L., *Gardenia* sp., *Gladiolus* sp., *Lantana* sp., *Lactuca sativa* L., *Rosa* sp., *Tithonia* sp. and *Tridax procumbens* L.

Frankliniella inutilis f. *adadusta* Moulton (1948:74) from Orizaba, Mexico, was treated as a junior synonym of *F. inutilis* by Jacot-Guillarmod (1974:794) but restored as a distinct species, *F. adadusta*, by Sakimura and O'Neill (1979:6). This species is known only from the lectotype and a paralectotype male, as designated by Sakimura and O'Neill (1979:6). In my opinion, the lectotype is a junior synonym of *F. simplex* Priesner (1924:532), **NEW SYNONYMY**, based on a comparison with a specimen of *F. simplex* identified by Priesner. The paralectotype, however, is another species, *F. reticulata*. Furthermore, *F. simplex* f. *celata* Priesner was treated as a junior synonym of *F. simplex* by Jacot-Guillarmod (1974:816). At my request, R. zur Strassen examined the types and confirmed that the synonymy was correct (pers. comm.).

The body of *Frankliniella simplex* is brown, antennae are brown except for a lighter brown segment III which is yellowish brown in basal one-third, forewings are completely brown except for a pale subbasal spot, and legs are brown except the foretibiae which are yellowish brown with margins brown. Pedicel of antennal segment III is either not enlarged or has a small enlargement. Interocellar setae on the head are separated by slightly more than a diameter of the anterior ocellus and are positioned on or slightly anterior to an imaginary line drawn between the anterior margins of the posterior ocelli. Abdominal tergite VIII has a complete posteromarginal comb, and B1 setae on tergite IX are about as long as segment X. Males of *F. simplex* have small, oval glandular areas which are less than twice as wide as long on sternites III–VII.

Frankliniella simplex is known only from Mexico and is often found on carnations, *Dianthus caryophyllus* L. Other recorded hosts are *Ananas comosus* (L.), *Celosia* sp., *Chrysanthemum* sp., *Dahlia* sp., *Gladiolus* sp., *Pisum* sp., *Rosa* sp., *Senecio* sp., *Tagetes* sp., and *T. lucida* Cav.

The primary types of *F. fuscipennis*, *F. inopinata* and *F. inutilis* f. *adadusta* are deposited in the Thysanoptera Collection of the U.S. National Museum of Natural History located at Beltsville, Maryland, not in the California Academy of Sciences as indicated by Jacot-Guillarmod (1974:779, 782, 794).

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**TAXONOMIC AND BIOLOGICAL NOTES ON
NORTH AMERICAN SPECIES OF *ELATOPHILUS* REUTER
(HEMIPTERA: HETEROPTERA: ANTHOCORIDAE)**

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Abstract.—There are 18 species in the wide-ranging genus *Elatophilus* Reuter. Five species are known predators of species of the scale genus *Matsucoccus* Cockerell. Several species of *Elatophilus* occur outside the range of *Matsucoccus*, suggesting other prey besides *Matsucoccus* may be involved, perhaps aphids.

The anthocorid genus *Elatophilus* Reuter is Holarctic and contains 18 species, eight of which are found in North America. These predaceous anthocorids occur only on coniferous trees and chiefly on species of *Pinus* L., although they have been recorded from other genera such as *Abies* Mill. and *Picea* Dietr. (Kelton, 1976).

Several species of *Elatophilus* have been associated with the magarodid scale genus *Matsucoccus* Cockerell. Some species of this genus are pests of pine in both the Old and New World [e.g., *M. feytaudi* Ducas in Europe (Biliotti and Riom, 1967) and *M. resinosae* Bean and Godwin in eastern United States (Drooz, 1985)]. For some of these scales, species of *Elatophilus* have been documented as their predators [e.g., *E. nigricornis* (Zetterstedt) (Pericart, 1972) and *E. inimicus* (Drake and Harris) (Lusier, 1965)].

We had completed a manuscript (Lattin and Stanton, 1992) on the Anthocoridae associated with *Pinus contorta* Doug. ex Loud., including a review of several species of *Elatophilus*, when the paper by Mendel et al. (1991) appeared. They presented an interesting summary of information on this genus, documented five species as specialized predators of *Matsucoccus* spp. and proposed a coevolutionary relationship with pine bark scales. One of these, *E. inimicus*, occurs in North America where it is a predator of the red pine scale, *M. resinosae* Bean and Godwin. In examining the information Mendel et al. presented for the eight North American species of *Elatophilus*, we found that some corrections were needed to evaluate their hypothesized *Elatophilus*-*Matsucoccus*-*Pinus* linkage. These are detailed in the text that follows.

TAXONOMIC AND BIOLOGICAL INFORMATION

Elatophilus antennatus Kelton

This species was described from four females collected at San Cristobal, Chiapas, Mexico (Kelton, 1976). No other records of this species have been reported in the literature. Because of its location, it was not included by Henry (1988) in the catalog

of North American Heteroptera. Mendel et al. (1991), citing only Kelton (1976), reported it from Mexico and Arizona, apparently the latter location in error. As these authors indicated, the species was collected by Kelton on *Pinus oocarpa* Schiede which occurs only in Mexico (Critchfield and Little, 1966). This species belongs to the subsection *Oocarpae* Little and Critchfield, a section that includes such species as *P. radiata* D. Don, *P. attenuata* Lemm., *P. muricata* D. Don, *P. patula* Schiede and Deppe, *P. greggii* Engelm. and *P. pringlei* Shaw (Critchfield and Little, 1966).

Elatophilus brimleyi Kelton

Kelton (1977) described this species from a single female collected in Prince Edward County, Ontario, Canada, but provided no biological or ecological information. Kelton included the species in his 1978 publication but added no new information. Henry (1988) cited the Ontario record in the catalog and placed the species in the nominate subgenus. Mendel et al. (1991) suggested that *Pinus strobus* L. might be the host tree and the prey species, *Matsucoccus macrocitrices* Richards. There are four native species of *Pinus* that occur at or close to the type locality in Ontario besides the introduced species, *P. sylvestris* L. (Little, 1979). Each of these pines might have species on *Matsucoccus* that are potential prey.

Elatophilus dimidiatus (Van Duzee)

This species was described by Van Duzee (1921) (in *Anthocoris*) from three females collected in northern California; no host data were included. Drake and Harris (1926) included one specimen from the type series in describing the new species *Temnostethus fastigiatus*, based on additional specimens from California. Kelton (1976) placed *A. dimidiatus* in the genus *Elatophilus* and mentioned the habitat was unknown. Henry (1988) reported California as the only locale and placed the species in the nominate subgenus. Although Mendel et al. (1991), citing Kelton (1976), listed an unknown species of *Pinus* as a possible host and *Matsucoccus* spp. as the prey, a question mark should be placed in front of *Matsucoccus* in their table because no prey information is yet available for this anthocorid.

We have collected *E. dimidiatus* at several localities in California on *Pinus contorta murrayana* (Grev. and Balf.) Engelm. and in Oregon on *P. ponderosa* Dougl. ex Laws. (Lattin and Stanton, 1992), but we have not confirmed any prey species. Furniss and Carolin (1977) cited only *Matsucoccus bisetosus* Morrison on *Pinus contorta* but other Homoptera occur on this host, including the pine needle scale, *Chinoaspis pinifoliae* (Fitch) (Diaspididae), and species of the aphid genera *Cinara* Börner and *Essigella* del Guercio, and species of *Pineus* Shimer (Phylloxeridae). These two authors also listed *M. bisetosus* and *M. fasciculensis* Herbert from *Pinus ponderosa* in Oregon.

Elatophilus inimicus (Drake and Harris)

Drake and Harris (1926) described this species, without host or prey information, from a female collected at Taghanic, Ithaca, New York (as a species of *Xenotracheiella* Drake and Harris). Kelton and Anderson (1962) placed *Xenotracheiella* into synonymy with *Elatophilus*. Kelton (1976) synonymized *X. vicaria* Drake and Harris

(1926) with *E. inimicus* (Drake and Harris) [not *E. vicarius* Kelton and Anderson as stated by Mendel et al. (1991) and parentheses should be placed around *E. inimicus* (Drake and Harris) because the species was described in *Xenotracheliella*]. No host or prey information was given for *X. vicaria*, described from Marquette, Michigan, by Drake and Harris (1926).

Kelton (1976) added records from Manitoba, Ontario, Quebec, Connecticut, and North Carolina (in addition to previous Michigan and New York records), stated that *Pinus banksiana* Lamb. was the host plant, but suggested other species of conifers as possible hosts. His only prey information was "It preys on the small arthropods living in the bark." Kelton (1978) added no new information. Henry (1988) placed *E. inimicus* in the nominate subgenus *Elatophilus* Reuter.

Doane (1965) reported *E. inimicus* on *Pinus resinosa* Ait., and Lussier (1965) added *P. rigida* Mill. and *P. sylvestris*. Apparently, *E. inimicus* has been found on *P. resinosa* only outside the natural range of the tree where it is found in plantations. These are the sites where populations of the red pine scale, *M. resinosa*, were first discovered and associated with *E. inimicus*. Drooz (1985) reported this bug "... on pines" without specific host names but said it occurred with several species of *Matsucoccus*. Mendel et al. (1991) listed *P. banksiana*, *P. resinosa* and *P. rigida* as host plants.

Doane (1965) cited *E. inimicus* (as *X. inimica*) as a predator of *M. resinosa* in Connecticut. Lussier (1965) detailed its role as a predator of *M. resinosa*. He also stated that the bug occurs with *M. gallicolus* Morrison on *Pinus rigida* in Massachusetts (no actual feeding was reported) in association with aphids and mites, and in Connecticut on *P. sylvestris* in the absence of *Matsucoccus*. Mendel et al. (1991) reported *M. gallicolus* (on *P. banksiana* and *P. rigida*) and *M. matsumurae* Kuwana (on *P. resinosa*) as the prey, but because no actual feeding was observed on *M. gallicolus*, a question mark should be placed before the name in their table. Since *Pinus banksiana* is one of the host plants (Kelton, 1978), one might add *Matsucoccus banksianae* Ray and Williams, with a question mark in front, to the list of possible prey since the scale occurs close to the bug's known range of the anthocorid bug (Ray and Williams, 1991). Drooz (1985) stated that *M. gallicolus*, the pine twig gall scale, is found on *Pinus echinata* Mill., *P. glabra* Walt., *P. ponderosa*, *P. pungens* Lamb., *P. resinosa*, *P. rigida*, *P. taeda* L., and *P. virginiana* Mill. He did not indicate whether the scale occurred on jack pine (*P. banksiana*) (but see Ray and Williams, 1991).

Mendel et al. (1991) listed *M. matsumurae* on *P. resinosa* as the prey of *E. inimicus* in North America, but there is question as to whether this scale actually occurs in the Nearctic Region. All prior references, except that of Morrison (1939), have cited *M. resinosa* Bean and Godwin as the species on red pine (Doane, 1959, 1965; Lussier, 1965; Ray and Williams, 1984; Drooz, 1985). Kosztarab and Kozar (1988) gave the distribution of *M. matsumurae* as Trans-Palearctic, extending from England to Japan and found on various Old World pines. Morrison (1939) stated that he had reported *M. matsumurae* from Alabama (1928) but he used these specimens in describing the new species of *M. alabamiae* Morrison (1939). Miller and McClure (1984) discussed problems in identifying *M. resinosa* using female sex pheromones. Additional work on this problem is underway (D. R. Miller, pers. comm., 19 November 1991). M. L. Williams (pers. comm., 18 November 1991) also indicated there is still no positive identification of *M. matsumurae* from North America and that *M. resinosa* is def-

initely a synonym of *M. matsumurae*. Because there apparently is no definite record of *M. matsumurae* from the United States, the citation by Mendel et al. (1991) should be changed to *M. resinosa*. There are no references to this usage in the three references they cite (i.e., Lussier, 1965; Kelton, 1976, 1978). However, we do note that Mendel et al. (1991) reported *M. matsumurae* as prey of *Elatophilus nipponensis* Hiura on *Pinus densiflora* Sieb. and Zucc. and *P. thunbergiana* Franco in South East Asia.

Elatophilus minutus Kelton

Kelton (1976) described this species from Laniel, Quebec, and included specimens from Alberta, Manitoba, Ontario, and Saskatchewan in the type series; specimens collected on young jack pine (*Pinus banksiana*) were noted without localities. *Pinus banksiana* ranges throughout the region of the general collection localities (Critchfield and Little, 1966). Kelton (1978) repeated this information, added that specimens were active on the trees, but gave no specific prey information. Henry (1988) placed *E. minutus* in the nominate subgenus.

Mendel et al. (1991) repeated most of the above information, omitting Alberta and Saskatchewan from the distribution, and reported *Matsucoccus banksianae* as prey. A question mark should be placed before the prey citation since actual feeding has not been observed. *Matsucoccus banksianae* is known only from Cass County, and Ely, Minnesota, where it was collected on *Pinus banksiana*. This is close to the reported range of *E. minutus*, but as yet the anthocorid and scale have not been collected together.

Elatophilus oculatus (Drake and Harris)

Drake and Harris (1926) described this species (as *Xenotrachelielliella oculata*) from a male collected at Williams, Arizona, with no biological information. Kelton and Anderson (1962) placed *X. oculata* in *Elatophilus*. Kelton (1976) included *E. oculatus* in his generic review, stating he saw only the type specimen, although he added that the species was collected on *Pinus ponderosa*, he did not give the origin of that information. *Pinus ponderosa scopulorum* Engelm. is found near Williams, but so are at least three other species of *Pinus* including *P. monophylla* (Torr. and Frem.) Although Mendel et al. (1991) repeated Kelton's (1976) information, a question mark should be placed before the host because no positive record exists. Henry (1988) placed *E. oculatus* in the nominate subgenus.

Elatophilus pinophilus Blatchley

Blatchley (1928) described this species from a single female collected at Royal Palm Park (now Everglades National Park), Florida, noting it had been collected from "... the top of a dead and fallen pine." Kelton (1976) was unable to locate Blatchley's type when he reviewed the genus *Elatophilus*. Henry (1988) listed Florida as the only known locale. Blatchley (1928) placed *E. pinophilus* in the subgenus *Euhadrocerus* Reuter and at present is the only North American species included in that taxon even though several other North American species have enlarged antennae (Henry, 1988). Four European species belong to this subgenus (Pericart, 1972).

Mendel et al. (1991) listed *Matsucoccus alabama* (sic) Morrison (*M. alabamiae* is correct) and *M. gallicolus* as possible prey. *Matsucoccus alabamiae* is known only

from Alabama, on *Pinus* sp. (Morrison, 1939). Ray and Williams (1984) indicated that *M. alabamiae* feeds on pines of the subsection *Australes* without citing species. Little (1979) listed seven species of *Pinus* from Florida; of these, six belonged to the subsection *Australes* and only *P. clausa* (Chapm.) Vasey belongs to the subsection *Contortae*. *Matsucoccus gallicolus* is widespread in eastern and southeastern United States and has been recorded from five species on *Pinus* (Morrison, 1939). Ray and Williams (1984) mentioned only that this scale feeds on a variety of pines.

Elatophilus pullus Kelton and Anderson

This species was described from southeastern British Columbia and central Oregon from specimens collected on *Pinus ponderosa* (Kelton and Anderson, 1962). Anderson (1962) provided biological information on *E. pullus*, including nymphal development in the laboratory and the field, and noted that overwintering occurs as fifth instar nymph in British Columbia. He gave the phenology of the adults in spring, stating males die within a month of appearance. This may explain the preponderance of females collected and why Pericart (1967) also notes the rarity of *Elatophilus* males. Kelton (1976) added no new information but (1978) reported it from Alberta and added *Pinus contorta*, *P. flexilis* James, and *Picea glauca* (Moench) Voss as hosts. Evans (1983) reported it from yellow pine (*P. ponderosa*) in southern British Columbia. Henry (1988) placed *E. pullus* in the nominate subgenus.

Mendel et al. (1991) doubted the validity of Anderson's (1962) record of rearing *E. pullus* nymphs on the filbert aphid *Myzocallis coryli* Goeze, stating that development instead might have resulted from cannibalism. They also challenged Sands' (1957) statement that *E. nigricornis* (Zetterstedt) feeds on conifer aphids in the United Kingdom. Cobben and Arnoud (1969) stated that additional work was needed to clarify the discrepancy between feeding habits of *E. nigricornis* in the northern and southern portions of its range. Woodroffe (1969) mentioned morphological differences between the populations of this species in Scotland and those from southern England, noting the latter may be derived from the European Continent. There is the possibility that other prey are involved.

Mendel et al. (1991) listed *Matsucoccus bisetosus* Morrison as possible prey of *Elatophilus pullus* on *Pinus ponderosa* and *P. contorta*, and *M. acalyptus* Herbert as possible prey on *Pinus flexilis*. According to Furniss and Carolin (1977), *M. bisetosus* occurs on *P. ponderosa*, *P. jeffreyi* Grev. and Balf., *P. contorta*, *P. sabiniana* Dougl. and *P. radiata* D. Don, whereas *M. acalyptus* is found chiefly on the pinyon pines *P. edulis* Engelm. and *P. monophylla* Torr. and Frem., *Pinus balfouriana* Grev. and Balf., *P. aristata* Engelm. and *P. lambertiana* Dougl.; *M. paucicatricis* Morrison is found on *P. flexilis*. Most of these pines occur south of the known range of *E. pullus*. Unruh and Luck (1987) studied *M. acalyptus* on *P. monophylla* but did not mention *Elatophilus*.

DISCUSSION AND CONCLUSIONS

The anthocorid genus *Elatophilus* is a wide-ranging taxon with 18 known species. Some have been recorded as predators of the margarodid scale genus *Matsucoccus*. Both bug and scale are found chiefly on pines (Mendel et al., 1991). They suggested that species of *Elatophilus* prey only on species of *Matsucoccus*. While this is possible, only five of the eighteen species of *Elatophilus* have been verified as *Matsucoccus*

predators. Moreover, there is evidence that prey other than *Matsucoccus* may be involved (Anderson, 1962; Cobben and Arnoud, 1969; Sands, 1957).

The map presented by Mendel et al. (1991) shows that a very substantial portion of the range of *Elatophilus* in Europe and of northern Asia lies outside of the range of *Matsucoccus*. The entomofauna of Europe is especially well known, including the Anthocoridae (Pericart, 1972) and the Margarodidae (Kosztarab and Kozar, 1988). The absence of *Matsucoccus* in Norway, Sweden and Finland, for example, suggests that the *Elatophilus* occurring there have prey species other than *Matsucoccus*. However, their prediction that *Matsucoccus* occurs on Cyprus was substantiated by the 1991 collections of *M. josefi* Bodenheimer and Harpaz and *M. pini* Green (Mendel et al., 1991:505). Mendel et al. (1991) have presented an interesting hypothesis but considerably more evidence is required before it can be concluded that all species of *Elatophilus* feed only on species of *Matsucoccus*. Perhaps species of *Matsucoccus* will be collected in northern Europe after all.

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**A REVIEW OF THE GENUS *MELANOCORIS* CHAMPION
WITH REMARKS ON DISTRIBUTION AND
HOST TREE ASSOCIATIONS
(HEMIPTERA: HETEROPTERA: ANTHOCORIDAE)**

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Abstract.—The biogeographical and ecological characteristics of *Melanocoris pingreensis* (Drake and Harris), *M. nigricornis* Van Duzee, and *M. longirostris* Kelton are examined (Hemiptera: Heteroptera: Anthocoridae). A key to species, distribution maps and habitus figures are included. Although predaceous, each bug species usually is found on a particular species of conifer. Sometimes more than one bug species is on the same host species. Past migrations of these hosts, chiefly in response to climatic changes, may have influenced the present distribution of *Melanocoris*. The hosts included *P. contorta*, *P. flexilis*, *P. jeffreyi*, *P. monticola*, *P. ponderosa*, and *P. strobiformis*. Host species movements may have resulted in the species formation of *M. pingreensis*, presently known only from southeastern Wyoming and central Colorado. *Melanocoris nigricornis* occurs from southern British Columbia south through the Rocky Mountains to Colorado and south through the Cascade Mountains and Sierra Nevada Mountains to northern Baja California, Mexico. *Melanocoris longirostris* has a similar distribution but also occurs in southern Utah, Arizona, and southern New Mexico.

The different species of pines in western North America are widespread (Critchfield, 1957; Critchfield and Little, 1966) and many have a rich heteropteran fauna (e.g., Lattin and Stanton, 1992). We have sampled and collected the Anthocoridae on the different subspecies of lodgepole pine, *Pinus contorta* Dougl. ex Loud., *P. ponderosa* Dougl. ex Laws., and other associated conifer species (Lattin and Stanton, in press). Here we provide a review of the anthocorid genus *Melanocoris* Champion together with information on distribution and host plant associations of the included species.

Taxonomic considerations. Presently, four species are included in the genus *Melanocoris* Champion. They are found only in North America and only on coniferous trees. The type of the genus, *M. obovatus* Champion, was described in 1900 from the Los Altos region of Guatemala between 2,615 and 3,231 m (probably from pine) and is only known from this locale.

Van Duzee (1921) described *M. nigricornis* from the central and southern Sierra Nevada Mountains of California. It has been collected in northern Baja California, California, Oregon, Washington, southeastern British Columbia, northwestern Wyoming, and Colorado (Van Duzee, 1921; Anderson, 1962; Kelton and Anderson, 1962; Kelton, 1977, 1978; Henry, 1988). *Tetraphelps novitus*, described by Drake and Harris (1926) from Stonewall, Trinidad, and Estes Park, Colorado, was synonymized with *M. nigricornis* by Kelton and Anderson (1962).

Drake and Harris (1926) described *M. pingreensis* (as a species of *Tetraphelps*)

from Estes and Pingree Parks along the Front Range of the Rocky Mountains in northern Colorado. Kelton and Anderson (1962) transferred *pingreensis* to the genus *Melanocoris* Champion. Henry (1988) listed only Colorado in the catalog of Hemiptera. We have taken it in Estes Park, Larimer County, on Cucharas Pass in Las Animas County, Colorado, and in southeastern Wyoming near the Colorado border. It has not yet been reported from other localities nor has there been any additional information published on this species since it was described.

Melanocoris longirostris was described by Kelton (1977) from southeastern British Columbia, Colorado, Utah, New Mexico, and Arizona. We have examined other specimens from Oregon, Nevada, and California. Some morphological differences of these latter specimens suggest that they may represent another species. A revision of *Melanocoris* is needed to clarify the situation.

The species discussed here may be separated by the following key:

KEY TO *MELANOCORIS* SPECIES NORTH OF MEXICO

1. Dorsum dull, shagreened; pubescence long, especially on clavus and basal half of corium 2
- Dorsum shiny, polished; pubescence very short on clavus and basal half of corium *longirostris* Kelton (Fig. 2)
2. Length 2.5 mm; tip of rostrum reaches middle coxae *pingreensis* (Drake & Harris) (Fig. 1)
- Length 3.0 mm; tip of rostrum reaches anterior coxae *nigricornis* Van Duzee (Fig. 3)

Host plants. Species of *Melanocoris* usually occur on species of pines but have been taken from other species of conifers (Kelton, 1977, 1978). The allotype of *M. pingreensis*, a male, was collected on "pine" at Pingree Park, Colorado (Drake and Harris, 1926). While no specific host was cited for the Estes Park specimen, *Pinus ponderosa scopulorum* Engelm., the Rocky Mountain ponderosa pine, is the most common species in the area and is the likely host.

Kelton (1977, 1978) reported *M. longirostris* from British Columbia on *P. monticola* Doug. ex D. Don; from Colorado on *P. flexilis* James, *Picea glauca* (Moench) Voss and *Abies lasiocarpa* (Hook.) Nutt.; and from Arizona on *Pinus ponderosa* (presumably *P. ponderosa scopulorum*) and *P. strombiformis* Engelm.

Van Duzee (1921) described *M. nigricornis* from the Sierra Nevada Mountains of California collected on an unnamed pine and on *Pinus jeffreyi* Grev. and Balf., and Anderson (1962) added *Pinus ponderosa* Dougl. ex Laws. and *P. contorta latifolia* Engelm. from British Columbia and Oregon [NOTE: This would be the nominate subspecies, *P. ponderosa ponderosa* (Conkle and Critchfield, 1988)]. Kelton (1978) recorded this species on *Pinus sylvestris* L. and *Picea engelmanni* Parry ex Engelm. from British Columbia.

Prey. No specific insect prey has been identified for *M. pingreensis*. Specimens of *M. longirostris* from Corvallis, Oregon were recorded as feeding on *Pineus* sp., a member of the Phylloxeridae (Hemiptera: Homoptera) (see specimens examined). Furniss and Carolin (1977) summarized the biology of some species of *Pineus*. Anderson (1962) found *M. nigricornis* associated with the aphids *Essigella fusca* G. and *P. and Cinara* sp., and with the pine needle scale, *Phenacaspis pinifoliae* (Fitch). He

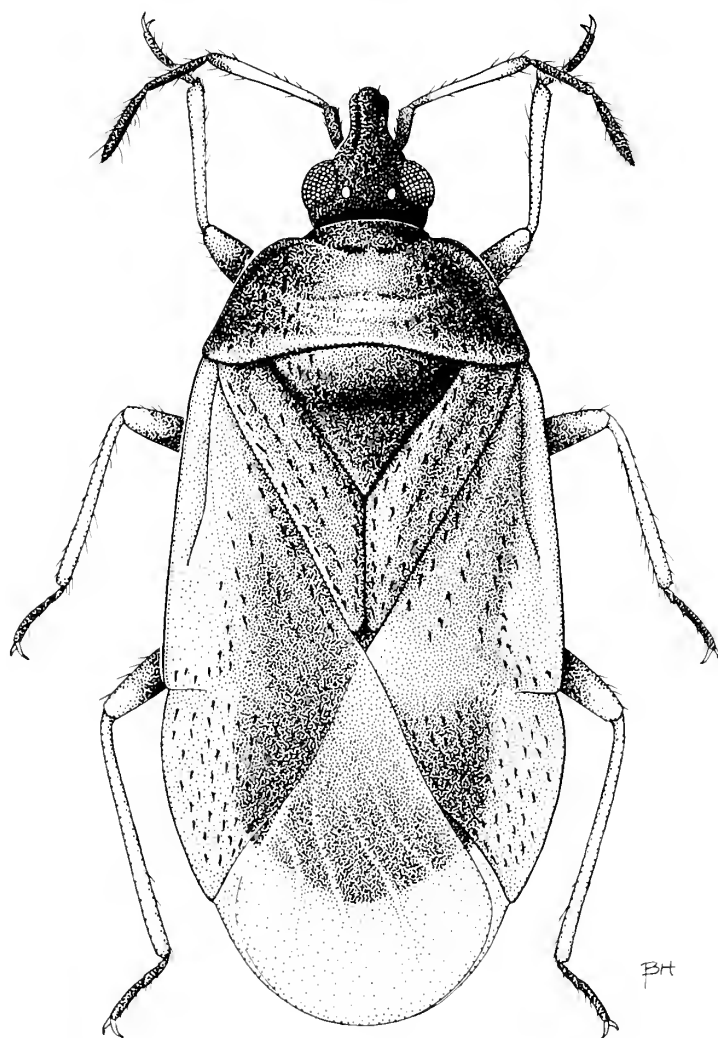


Fig. 1. *Melanocoris pingreensis* (Drake and Harris), female, Colo., Larimer Co., Estes Park YMCA Camp, ex *Pinus ponderosa* scapulorum.

reared this anthocorid in the laboratory on the filbert aphid, *Myzocallis coryli* (Goeze). Kelton (1978) reported a collection of *M. nigricornis* from *Pinus sylvestris* that had a heavy infestation of scale insects and from *P. contorta*, *P. ponderosa*, and *Picea engelmanni* that were infested with adelgids, aphids, and scale insects.

METHODS

Material presented here represents the results of our sampling on a regular basis from three sites in southeastern Wyoming in 1986 (see specimens examined). Spec-

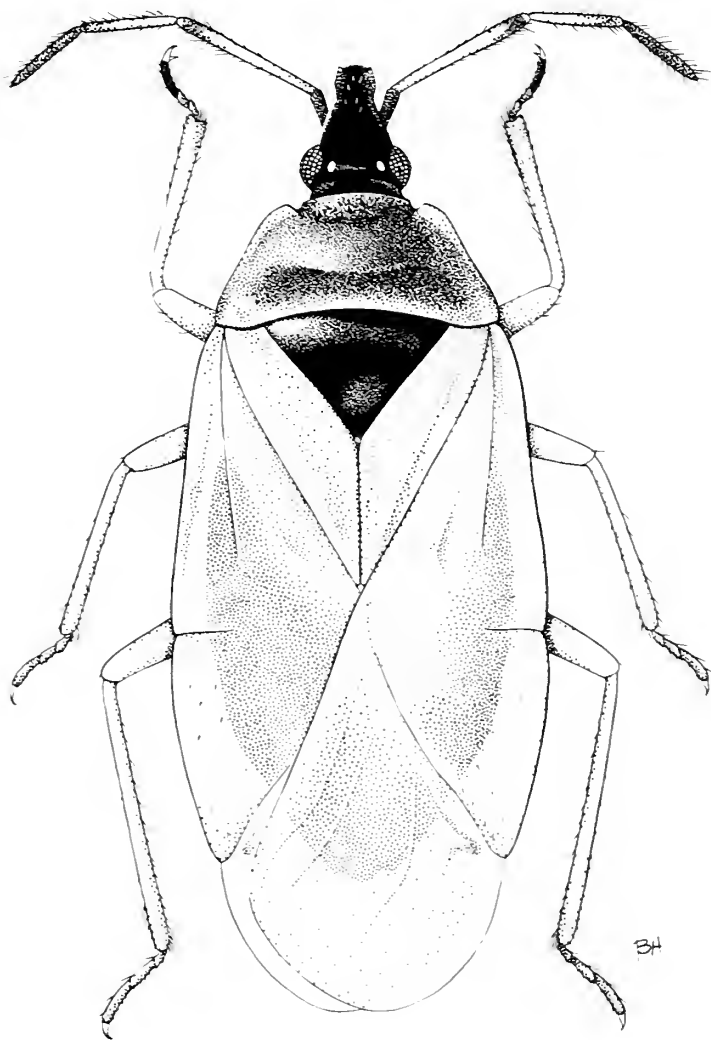


Fig. 2. *Melanocoris longirostris* Kelton, female, Colo., Larimer Co., Rocky Mt. Nat. Pk., ex *Pinus contorta latifolia*.

imens were collected by beating 20 branches onto a beating sheet where the insects were picked up with an aspirator. Branches continued to be beaten until no additional specimens appeared after ten individual beats. Additional collections were made in Colorado from the Estes Park region in 1990 and throughout Colorado in 1991 where special emphasis was placed upon collections from *P. contorta latifolia*, *P. ponderosa scopulorum*, and *P. aristata* Engelm. All specimens have been deposited in the Systematic Entomology Laboratory, Department of Entomology, Oregon State Univer-

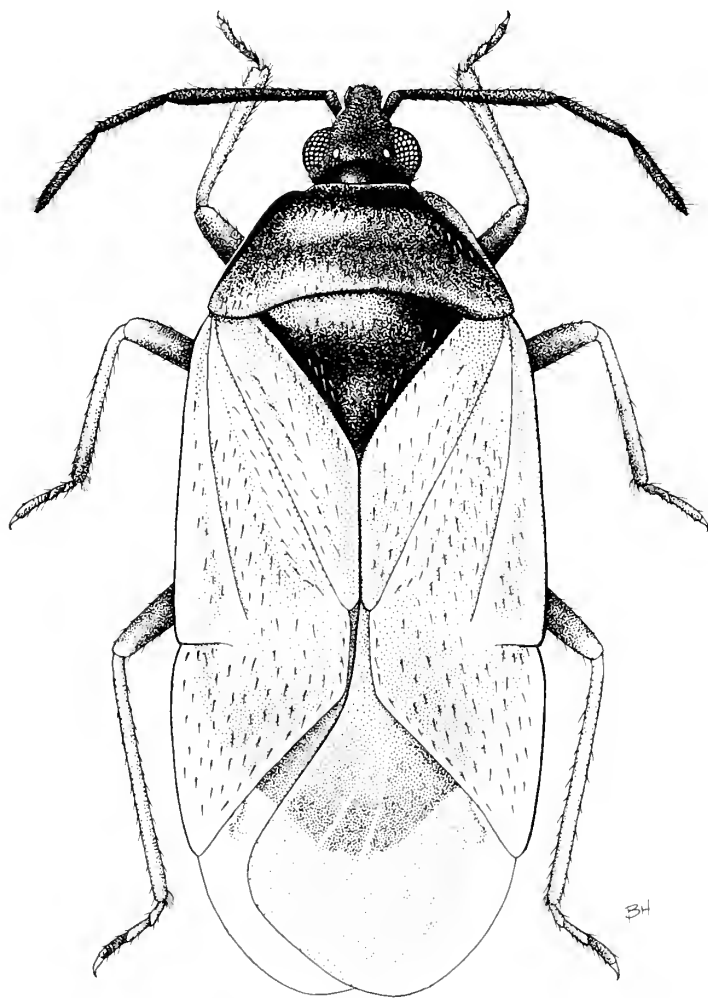
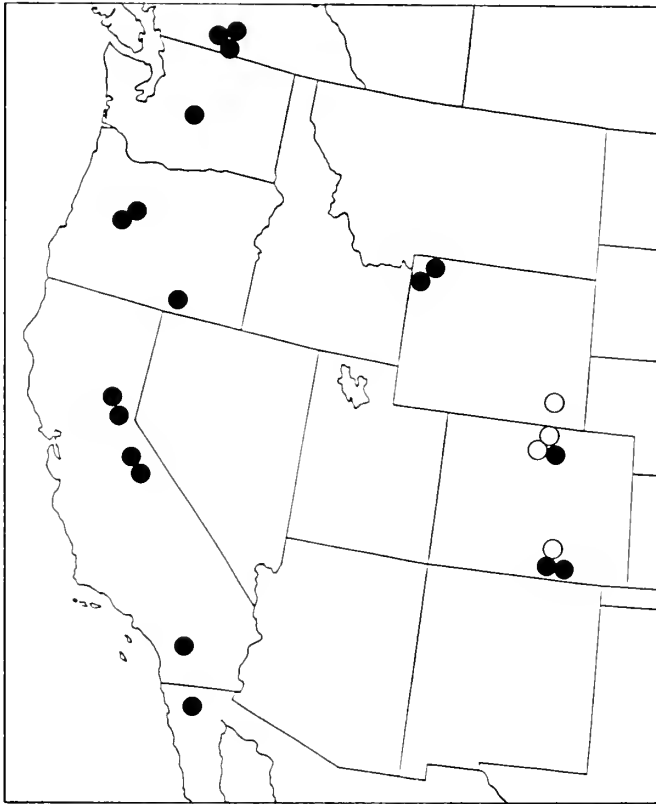


Fig. 3. *Melanocoris nigricornis* Van Duzee, female, Calif., Sierra Co., Tahoe Nat. For., FS Rd. 07, ex *Pinus contorta murrayana*.

sity, Corvallis. Records have been taken from the literature and from material in other collections where available.

RESULTS

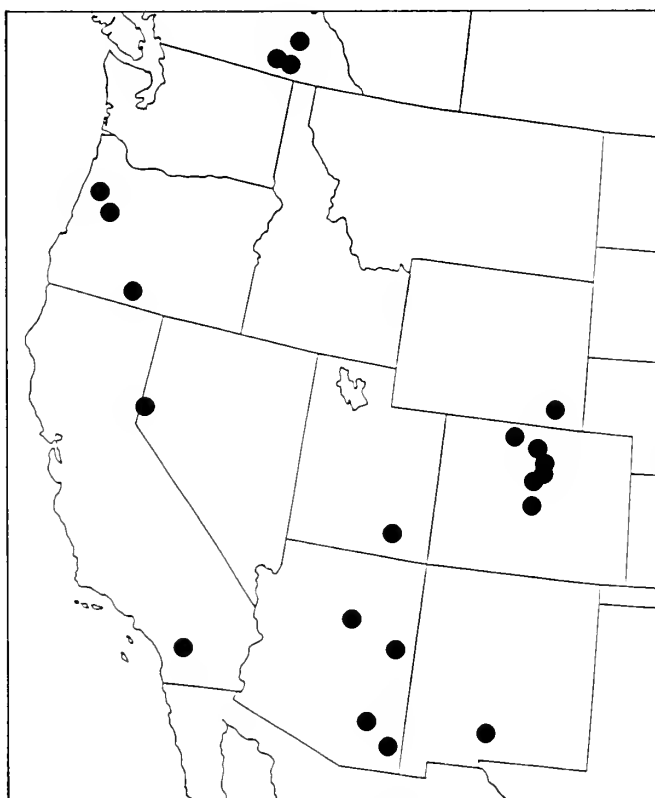
We have collected specimens of *M. pingreensis* in southeastern Wyoming and parts of adjacent Colorado from *Pinus ponderosa scopulorum* (see specimens examined). At present, this species is known only from this area of the Rocky Mountains at about 2,500 m elevation and has the most restricted distribution of the three species (Map 1).



Map 1. Distribution of *Melanocoris pingreensis* (○) and *M. nigricornis* (●).

Melanocoris longirostris was described from southeastern British Columbia, Colorado, Arizona, New Mexico, and Utah (Map 2). We have seen specimens from southeastern Wyoming and adjacent Colorado, Oregon, Nevada, and California. Most of the Colorado localities are in that portion of the Rocky Mountains close to the Wyoming locale. The Arizona, New Mexico, and Utah records come from scattered, high elevation sites (e.g., Mt. Lemmon, San Francisco Mts., Cloudcroft, and Henry Mts. respectively). *Melanocoris longirostris* has not been taken in the Yellowstone Park region of northwestern Wyoming where the usual host plant, *P. contorta latifolia* Engelm., is common.

Melanocoris nigricornis has the broadest range (Map 1). It was common on *P. ponderosa scopulorum* at Estes Park, and Drake and Harris (1926) reported it from "pine" at the Stonewall and Trinidad localities. *Pinus ponderosa scopulorum* is the common pine at Stonewall. Specimens of *nigricornis* were taken in northwestern Wyoming in Grand Teton and Yellowstone National Park on *P. contorta latifolia*. The Central Wyoming basins represent a substantial gap in the distribution of pine in the Rocky Mountains. It is probable that *M. nigricornis* also occurs in suitable habitats between northwestern Wyoming and southeastern British Columbia. We



Map 2. Distribution of *Melanocoris longirostris* (●).

have examined specimens from southeastern British Columbia (Princeton) taken on *P. contorta latifolia*. *Melanocoris nigricornis* extends southward from British Columbia through Washington, Oregon and California to northern Baja California, Mexico and was taken chiefly on *P. contorta* although recorded from several other coniferous hosts as well (*Pinus* spp. and *Picea engelmanni*).

Specimens examined. *Melanocoris pingreensis*: Colorado, Larimer Co., Estes Park YMCA Camp, 6 km SW Estes Park, 2,465 m, R13W T4N Sec 4, 26 September 1990, *P. ponderosa scopulorum*, Lattin, 4 females, 2 males; Estes Park, east end, 2,338 m, 1 September 1991, *P. ponderosa scopulorum*, Lattin, 9 females; Las Animas Co., 4 km S Cucharas Pass, 2,892 m, 5 September 1991, *P. ponderosa scopulorum*, Lattin, 4 females, 1 male. Wyoming, Albany Co., Medicine Bow Nat. For., Happy Jack Road, 19 km E Laramie, 2,500 m, R72W T15N Sec 25, 26 July 1986, *P. ponderosa scopulorum* (10 trees pooled), Stanton, 1 female.

Melanocoris longirostris: California: San Bernardino Co., above W end Big Bear Lake, R1W + T2W NW¼ Sec 34, 2,215 m, 8 June 1989, champion *P. contorta murrayana* (Grev. and Balif.) Engelm., Lattin, 3 females. Colorado: Larimer Co., Rocky Mt. Nat. Pk., 8.1 km W Estes Park, R13W T5N Sec 19, 2,677 m, 29 September

1990, *P. contorta latifolia*, Lattin, 1 female; Las Animas Co., 4 km S Cucharas Pass, 2,892 m, 5 September 1991, *P. aristata*, Lattin, 1 female. Nevada: Washoe Co., Galena Cr., Mt. Rose, 14 June 1964, Smith and Baker, 1 female. Oregon: Benton Co., Corvallis, OSU campus, 28 August 1959, *P. monticola*, feeding on *Pineus* sp. Mitchell, 22 females, 17 males; 1 July 1988 (some teneral) *P. monticola*, Asquith, 1 female, 1 male; Klamath Co., base of Gearhart Mt., 7 June 1959, *P. contorta murrayana*, Schuh, 1 female; Lane Co., H. J. Andrews Exp. For., 18 km NE Blue River, 18 August 1988, *P. monticola*, Asquith, 5 females, 2 males, 2 5th instar nymphs. Wyoming: Albany Co., Medicine Bow Nat. For., Happy Jack Road, 19 km E Laramie, 2,500 m, R72W T15N Sec 25; 25 and 27 July 1986, *P. contorta latifolia*, Stanton, 3 females; 9 July 1986, *P. flexilis* (10 trees pooled), Stanton, 1 female.

Melanocoris nigricornis: CANADA: British Columbia; 19.5 km W Princeton, 1,169 m, 31 July 1957, *P. contorta*, 1 male. MEXICO: Baja California Norte, 90 km E San Telmo, 18 April 1979, *P. contorta murrayana*, Lightfoot, 4 females, 2 males. UNITED STATES: California: Fresno Co., Pioneer Basin, 13 km W Tom's Place, 3,400 m, 27 October 1959, Schlinger, 1 female, (UCR); Mono Co., June Lake, Hwy 158, 16 June 1989, *P. contorta murrayana*, Lattin, 3 females; Sierra Co., Tahoe Nat. For., FS Rd. 07, 28 km W Hwy 89, 2,092 m, 16 July 1987, *P. contorta murrayana*, DiGiulio, 1 female. Colorado: Larimer Co., Estes Park YMCA Camp, 6 km SW Estes Park, 2,465 m, R13W T4N Sec 4, 26 September 1990, *P. ponderosa scopulorum*, Lattin, 3 females, 1 male; Las Animas Co., 4 km S Cucharas Pass, 2,892 m, 5 September 1991, *P. ponderosa scopulorum*, Lattin, 1 female. Oregon: Deschutes Co., Three Crks. Mdw., 26 km S Sisters, 2,065 m, 1 September 1977, *P. contorta murrayana*, Lattin, 3 males; Three Crks. Lk., 28 km S Sisters, 2,100 m, 14 June 1990, *P. contorta murrayana*, Asquith and Lattin, 8 females; Black Butte Ranch, 12 km NW Sisters, 1,015 m, 24 March 1990, *P. sylvestris*, Lattin, 3 females, 3 males; Linn Co., Big Lake, 1,431 m, 1 October 1979, *P. contorta murrayana*, Lattin, 4 females. Washington: Kittitas Co., 8 km W, 5 km S of Cle Elum, 6 June 1970, Harris, 1 female. Wyoming: Park Co., Yellowstone Nat. Pk., 8 km S Tower Falls, 2,262 m, 17 September 1980, *P. contorta latifolia*, Lattin, 2 females; Teton Co., Grand Teton Nat. Pk., 2,123 m, 18 September 1980, *P. contorta latifolia*, Lattin, 3 males.

DISCUSSION

Host range. Although Anthocoridae are chiefly predaceous, they often show remarkable fidelity to given host plants, and in this case, the genus *Melanocoris* to coniferous trees. Elsewhere, we have reported 18 species of anthocorids representing 10 genera found on *P. contorta* (Lattin and Stanton, 1992). Although several were likely visitors from nearby vegetation, most occurred consistently on that tree species. Some Anthocoridae are known to feed upon plant materials besides being predaceous (Lattin and Stanton, 1992).

Melanocoris pingreensis is known only from *P. ponderosa scopulorum* and only from a restricted portion of this tree's range. *Melanocoris longirostris* is found on four species of pine and on *Picea glauca* and *Abies lasiocarpa* in the northern part of its range. *Melanocoris nigricornis* is found on four species of pines, including three subspecies of *P. contorta* and on *Picea engelmanni* in the northern portion of the bug's range. All three species of *Melanocoris* have been collected on *P. ponderosa*. *Melanocoris nigricornis* and *M. longirostris* have both been collected from *P. contorta*

latifolia and *P. c. murrayana* but only at two locales. Species overlap on specific hosts: *Melanocoris pingreensis* and *M. nigricornis* on *P. ponderosa scopulorum* in northern Colorado and *M. longirostris* and *M. nigricornis* on *P. contorta murrayana* in southern California. Such host association, combined with the very patchy distribution of some of the hosts, may result in speciation. It is interesting to note that both *M. pingreensis* and *M. nigricornis* were taken from the same tree in Estes Park in September, 1990. Detailed host data from specimens of *M. nigricornis* in that general area are scanty. It occurs on *Pinus contorta latifolia* in northwestern Wyoming but did not appear in our samples from this host in southeastern Wyoming, and was reported only from "pines" from Stonewall and Trinidad, Colorado (but see note earlier in this paper) (Drake and Harris, 1926). Information about the factors determining the occurrence and distribution of insects on these hosts will be helpful.

Geographical distribution. Thus far, *Melanocoris pingreensis* has the most limited geographical distribution and is known only from southeastern Wyoming in the Laramie Range east of Laramie, and in the Front Range and Sangre de Cristo Mountains of the Rocky Mountains of Colorado (see specimens examined). Recent collecting (1991) on this host in the mountains of central and western Colorado failed to produce *M. pingreensis* although it was collected at Estes Park and at Cucharas Pass (see specimens examined). The present distribution of *M. pingreensis* probably dates back to the post-Pleistocene with the increased isolation and fragmentation of the populations of its host plant. Because of the presumed antiquity of its host plant (see below), the speciation event of the bug might be considerably older. The dynamics of the vegetation in this region of the Rocky Mountains during the Pleistocene have been the subject of considerable interest and research (see for example Short, 1985; Fall, 1985; Adams, 1983; Wells, 1963; Wells, 1970; Jacobs, 1985).

Hengeveld (1989) documented the movement of different elements of the biota across the landscape. In the case of *Pinus ponderosa*, the use of fossil material from the Pleistocene deposits and post-Pleistocene pack-rat middens has provided information about the presence and movement of some parts of the flora (J. L. Betancourt, pers. comm. 1991). Certainly, *P. ponderosa* has been a mobile species, but its fossil record is still imperfectly known (Martin, 1963; Wells, 1970; Cole, 1983; Van Devender and Toolin, 1983; Van Devender, 1990a, b).

Conkle and Critchfield (1988) outlined the genetic variation throughout the range and likely evolutionary history of *Pinus ponderosa*. Citing Axelrod (1986), they reported a cone fragment attributed to *P. ponderosa scopulorum* from Creede, Colorado, dated at 26.5 millions years. According to these authors, the geological history of *P. ponderosa* may extend back 50 million years. Linhart (1988) provided information on the genetic variability of *P. ponderosa scopulorum* and discussed variation in space and time and the interactions between the host tree and different organisms. He cited dwarf mistletoe (*Arceuthobium*) and bark beetles (*Dendroctonus* spp.) as examples of species-specific associations with the tree.

Conkle and Critchfield thought that the most likely origin of modern ponderosa pine was in Mexico and resulted in two different varieties—the western form found in southern California (Cole, 1983) and the eastern form found in the Southwest (Van Devender and Toolin, 1983; Van Devender, 1990a, b), the former derived from the west coast and the latter from the central Mexico populations.

The evidence from pack-rat middens dated at 40,000–50,000 years indicated pon-

derosa pine was not present in southwestern United States until *after* the last glacial epoch ($\pm 10,500$ years) (Van Devender, 1987) and Conkle and Critchfield concluded that although ponderosa pine had an extensive geographic range during warm interglacial times, it may have been restricted to only a few refugia during full-glacial periods. If so, then such refugia may have provided the isolating conditions that resulted in allopatric speciation of insects associated with the tree—e.g., *Melanocoris pingreensis*. Obviously, with such a long geological history, earlier events may have resulted in such speciation.

Cronkle and Critchfield (1988) also suggested that ponderosa pines are very recent colonizers in much of their present range, perhaps within the last 6,000–8,000 years. According to these authors—“If significant climatic warming during the Xerothermic period 3,000 to 8,500 years ago was a primary reason for ponderosa’s massive range extensions, the existence of races could trace to a few, relatively restricted progenitor populations.” Wells (1970) reported macrofossils of *P. ponderosa scopularum*, dated at 1860 and 4060 B.P. from the southwest corner of the Laramie Basin, Wyoming, where the tree still exists. Elliott-Fisk, Adkins, and Spaulding (1983) provided a critical review of the work of Wells (1970) and suggested that the earlier forest/woodlands were confined to sandstone outcrops as outliers of the montane forest of Medicine Bow Mountains. Collecting on *P. ponderosa scopularum* on the scarps of eastern Wyoming, as well as other widely scattered and isolated populations of *P. p. scopularum* from throughout the southwest, will likely yield distribution records of interest and help clarify some distributional aspects.

According to Conkle and Critchfield (1988), there are two major races of *P. ponderosa scopularum*: the Rocky Mountain race found today from southern Utah and Colorado north to Wyoming, Montana and North and South Dakota; and a southern race found in southern Utah and Colorado, Arizona and New Mexico. The concept of race used by Conkle and Critchfield appears very similar to the concept of subspecies used elsewhere.

Hawksworth and Shaw (1988), discussing diseases of ponderosa pine, included a map of the distribution of the two major species of dwarf mistletoe found on ponderosa pine—*Arceuthobium campylopodum* Engelm. on *P. p. ponderosa* and *A. vaginatum cryptopodum* (Engelm.) Hawks. and Wiens on *P. p. scopularum*. Of special interest is the fact that the species of mistletoe found on *P. p. scopularum* occurs only in the southern portion of the tree’s range suggesting that the tree has expanded its range more rapidly than the parasite. Hawksworth and Wiens (1984) reported that the southern portion of the range of *A. v. cryptopodum* extended south to Chihuahua and Coahuila, Mexico where it is found on several other species of *Pinus*. There are parallels between the movement of this plant parasite of ponderosa pine and the movement of some of the associated insects, i.e., anthorcorids.

Steele (1988) outlined the ecological relations of ponderosa pine and discussed the differences in the environment occupied by both subspecies of the tree and the other plants associated with them. The map in his paper illustrated the extensive range presently occupied by *P. ponderosa*. The study of other groups of organisms associated with ponderosa pine may shed light on the complex history of this tree species.

Finally, Mexico almost certainly holds additional species of *Melanocoris*. Thorough collecting with close attention to host plant information and locale will clarify our knowledge of this genus of Anthorcoridae.

CONCLUSIONS

The patterns of distribution of three species of *Melanocoris* are the product of close association with several host tree species or subspecies. The widespread distribution of *Pinus ponderosa*, *Pinus contorta*, and *P. flexilis* has provided habitats for species of *Melanocoris*. Since the host plants do not offer a continuous habitat, but rather a widespread, highly patchy habitat, the occurrence of the anthocorids in widely separated localities suggests either extraordinary dispersal capabilities or close association, perhaps coevolution, with that host tree in geological time as the range of the tree expanded and contracted in response to pre- and post-Pleistocene events (C. Whitlock, pers. comm., 1991). The latter explanation seems more likely.

The fact that within the total range of the bug species there is often a regional association with different host trees—i.e., *Pinus monticola*, *Pinus contorta*, and *P. ponderosa* for *Melanocoris longirostris* (Map 2), or *Pinus ponderosa* and *P. contorta* for *M. nigricornis* (Map 1), and *P. ponderosa scopulorum* for *M. pingreensis* (Map 1)—suggests past constrictions and confinements on different host trees resulting in present day distributions. The restricted distribution of *M. pingreensis* suggests long isolation on some subset of *Pinus ponderosa*, or, less likely, it may represent the remnant of a once more widespread distribution. The presence of all three species of *Melanocoris* in the vicinity of Estes Park, Colorado provides a unique opportunity for biological and ecological studies.

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A KEY AND DIAGNOSES FOR MALES OF THE *INCURVIA* SPECIES-GROUP OF *ANTITEUCHUS* DALLAS WITH DESCRIPTIONS OF THREE NEW SPECIES (HEMIPTERA: PENTATOMIDAE: DISCOCEPHALINAE)

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Abstract.—A key and diagnoses are provided for the 21 described species in the *incurvia* species-group of the nominate subgenus of *Antiteuchus* Dallas. Three new species are described: *A. rufitarsus* from Venezuela, *A. englemani* from Ecuador and *A. rideri* from Brazil. *Antiteuchus ratcliffi* Engleman, 1983, is placed in the synonymy of *A. marmoratus* (Erichson, 1848). Lectotypes are designated for *A. pallescens* Stål and in the *parallela* species-group, *A. sepulcralis* (Fabricius).

In a revision of *Antiteuchus* Dallas, Ruckes (1964) characterized the genus, and its two subgenera, and divided the nominate subgenus into two species-groups, naming one the *parallela* group and the other the *incurvia* group. The species-groups were further defined by Engleman and Rolston (1983). Although a suite of features separate the two groups, the single apparently infallible character is the presence of a fringe of fine setae along the posterior margin of the last abdominal tergum in males of the *parallela* species-group, and the absence of this fringe in males of the *incurvia* species-group. The latter group originally contained 13 species, nine of which were new at that time. Engleman (1976, 1983 in Engleman and Rolston) described four additional species in the *incurvia* species-group and Rolston (1991) described another. Three more new species are described herein, and *Antiteuchus ratcliffi* Engleman, 1983 is placed in the synonymy of *A. marmoratus* (Erichson, 1848), bringing to 21 the known species of this species-group.

Most specimens of the *incurvia* species-group have been collected in the great basin drained by the Amazon River and its tributaries, or along the low lands of northern South America, with a single species, *A. cuspidatus* Ruckes, extending into the Panama Canal Zone. However, there are records of a few species of the *incurvia* species-group from several coastal states of Brazil extending from Bahia to Santa Catarina.

Nothing is known of the biology of these species other than a host record for *A. cuspidatus* of *Luehea seemanii* Tr. and Pl., family Tiliaceae, a deciduous tropical tree, a host record for *A. amplus* of cacao, and a host record of *Annona muricata* L., family Annonaceae, for *A. varians*.

KEY TO MALES OF *INCURVIA* SPECIES-GROUP OF *ANTITEUCHUS*

1. Posterior margin of last abdominal tergum with prominent mesial convexity or process (Figs. 15, 25, 28) 4
- Posterior margin of last abdominal tergum with weak mesial convexity at most (Figs. 1, 3, 6) 2

- 2(1). Foliate part of each paramere-head finely denticulate on superior part of posterior margin; lateral lobe bifurcate with parts directed in opposite directions (Fig. 2); second antennal segment about 0.25 length of third segment, all of last segment sordid ivory *graziae* Engleman
- Foliate part of each paramere-head bearing carinae on mesial face, superior part of posterior margin entire; lateral lobe bifurcate with parts similarly oriented (Figs. 5, 8); second antennal segment about 0.5 length of third, last segment bicolored 3
- 3(2). Series of parallel carinae extending onto ventromesial lobe; axis of ventromesial lobe and axis of paramere shaft approximating right angle (Fig. 4) .. *ruckesi* Rolston
- Series of parallel carinae extending to posteroventral angle of foliate part of each paramere-head, but not involving ventromesial lobe (Fig. 7); ventromesial lobe recurved, nearly parallel to axis of paramere shaft *nebulosus* Ruckes
- 4(1). Tergal process bifid with deep, mesial cleft (Figs. 10, 15) 5
- Tergal process either entire apically or at most shallowly notched (Fig. 28) 6
- 5(4). From caudomesial view, mesial lobe of each paramere T-shaped apically (Fig. 12); first and second antennal segments subequal in length *peruensis* Ruckes
- From caudomesial view, mesial lobe of each paramere concavely cupped (Fig. 17); second antennal segment two-thirds length of first *rolstoni* Engleman
- 6(4). Tergal process convexly produced (Fig. 23) 7
- Tergal process elongated (Figs. 25, 28) 8
- 7(6). Ventromesial lobe of each paramere bearing about six transverse carinae (Fig. 22) *rufitarsus*, new species
- Parameres without such carinae *bartletti* Ruckes
- 8(6). Tergal process abruptly narrowed subapically, reduced size continuing to narrowly rounded apex (Fig. 25) *amplus* (Walker)
- Tergal process digitiform, or subquadrate, or subrectangular or expanded apically 9
- 9(8). Tergal process conspicuously expanded apically (Figs. 28, 32) 10
- Tergal process digitiform or subquadrate or subrectangular with little or no apical expansion 11
- 10(9). Apex of tergal process rounded and mesially notched (Fig. 28); lateral pygophoral appendages each with pincher-shaped projection from mesial surface (Fig. 29)
- Apex of tergal process truncate (Fig. 32); lateral pygophoral appendages lacking projections *tessalatus* (Westwood)
- 11(6). Posterior margin of last abdominal tergum deeply excavated, either extending cephalad beyond base of tergal process or very strongly sinuous (Figs. 36, 41) ... 12
- Emargination of last abdominal tergum arcuate or moderately sinuous, not extending cephalad beyond base of tergal process 13
- 12(11). Last abdominal sternite with quadrate mesial projection from posterior margin; paramere-heads each with 4 acute lobes (Fig. 38) *geometricus* Engleman
- Posterior margin of last abdominal sternite without mesial projection; paramere-heads each with 3 lobes, dorsal lobe inverted cup with carinae on convex surface (Fig. 44) *englemani*, new species
- 13(11). Tergal process subequal to or shorter than its subapical width (Fig. 45) 14
- Tergal process much longer than its subapical width 15
- 14(13). Lateral pygophoral appendages toothed subapically from caudal view (Fig. 48) ...
- Lateral pygophoral appendages unarmed *pallescent* (F.)
- 15(13). Head of each paramere with 3 lobes 16
- Head of each paramere with 4 or 5 lobes 17

- 16(15). Head of each paramere with two well-separated mesial lobes (Fig. 51) *confinium* Ruckes
 – Head of each paramere with two lateral lobes joined basally and forming carina (Fig. 71) *rideri* new species
- 17(15). Mesial face of lateral pygophoral appendage straight from base to apex, not impressed, unarmed *marmoratus* (Erichson)
 – Mesial face of lateral pygophoral appendage curving mesad from base to apex, usually impressed, either terminating in hook or with carinate or toothed production at apex of ventral margin 18
- 18(17). Mesial lobe of each paramere head larger than other lobes (Fig. 55) *guianensis* Ruckes
 – Mesial lobe of each paramere head not exceeding all other lobes in size 19
- 19(18). Length of tergal process nearly 4 times its width at posterior margin of tergum (Fig. 57) *punctissimus* Ruckes
 – Length of tergal process less than twice its width at posterior margin of tergum 20
- 20(19). Tergal process somewhat tectiform dorsally (Fig. 60); tubercles on proctiger rather flat, posteriorly directed *varians* Ruckes
 – Tergal process flat dorsally, tubercles on proctiger triangular, erect *mimeticus* Ruckes

Antiteuchus graziae Engleman, 1983

Figs. 1, 2

Antiteuchus (Antiteuchus) graziae Engleman, 1983:185–187, figs. 12, 15, 20.

Diagnosis. Last abdominal tergum lacking mesial process on posterior border (Fig. 1); membrane extending entirely across posterior margin of tergum. Head of each paramere laminate, finely denticulate on superior part of posterior margin (Fig. 2); lateral lobe bifurcate with branches directed in opposite directions. Second antennal segment about one-fourth length of third; proximal third of fourth segment and all of last segment ivory.

Distribution. Brazil (Mato Grosso).

Comment. Of the three species lacking a pronounced tergal process, this species alone also lacks carinae on the parameres.

The male paratype and another male were examined.

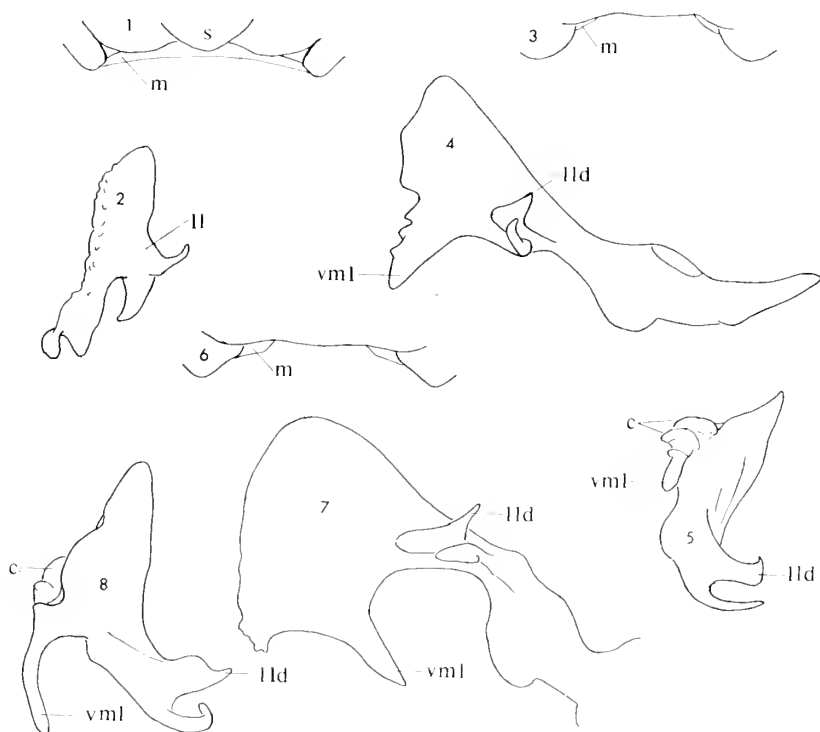
Antiteuchus ruckesi Rolston, 1991

Figs. 3–5

Antiteuchus ruckesi Rolston, 1991:235–238, figs. 1–6.

Diagnosis. Last abdominal tergum lacking mesial process on posterior border (Fig. 3); membrane reduced, apparent on each side only near connexival sclerite. Head of each paramere laminate; subparallel series of carinae on mesial face extending onto ventromesial lobe (Figs. 4, 5); axes of ventromesial lobe and axis of paramere shaft approximating right angle; lateral lobe bifurcate, branches similarly oriented basally. Second antennal segment about one-half length of third; basal three-tenths of fourth segment, basal one-half and apical one-tenth of last segment ivory. Dorsum variegated.

Distribution. Peru (Madre de Dios).



Figs. 1–8. Figs. 1, 2. *A. graziae*. 1. Posterior margin of last abdominal segment, dorsal view. 2. Right paramere, caudodorsal view. Figs. 3–5. *A. ruckesi*. 3. Posterior margin of last abdominal tergite. 4. Right paramere, excised, lateral view. 5. Right paramere-head, caudoventral view. Figs. 6–8. *A. nebulosus*. 6. Posterior margin of last abdominal tergite. 7. Right paramere, excised, lateral view. 8. Right paramere, caudal view. Symbols: c, carina; ll, lateral lobe; lld, lateral lobe, dorsal branch; m, membrane; s, scutellum; vml, ventromesial lobe.

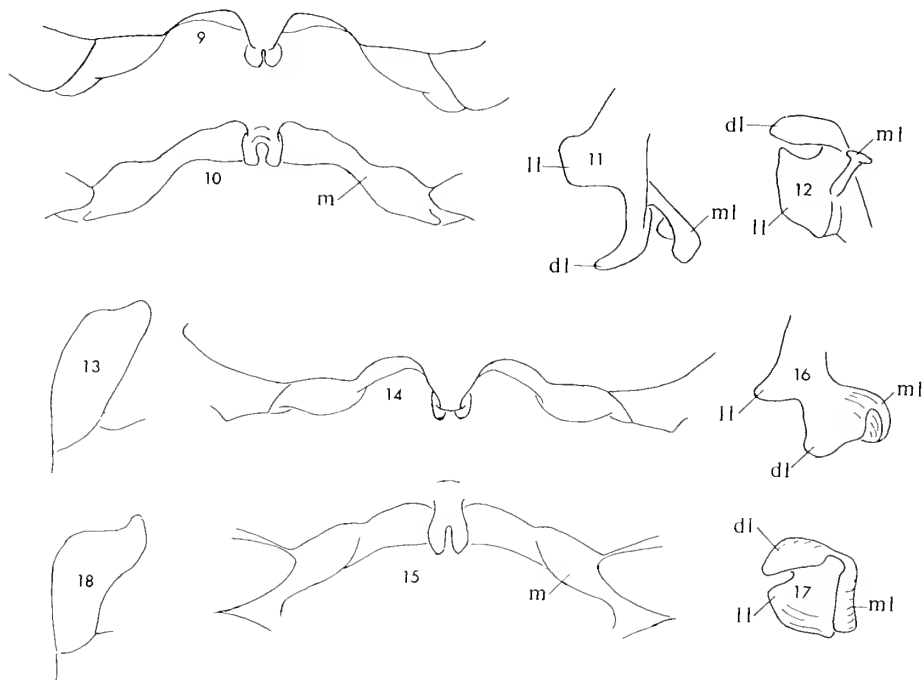
Comment. This and the following species are conspicuously variegated dorsally and otherwise similar excepting differences in the parameres.

Antiteuchus nebulosus Ruckes, 1964

Figs. 6–8

Antiteuchus (Antiteuchus) nebulosus Ruckes, 1964:84, 89–91, figs. 10, 53–55.

Diagnosis. Last abdominal tergum lacking mesial process on posterior border (Fig. 6); membrane reduced, apparent on each side only near connexival sclerites. Head of each paramere laminate; subparallel series of carinae on mesial face extending to posteroventral corner of lamina, not involving ventromesial lobe; ventromesial lobe recurved, nearly paralleling paramere-shaft (Figs. 7, 8); lateral lobe bifurcate, branches similarly oriented basally. Second antennal segment about four-tenths length of third; basal one-fourth of segment four and broad basal band on segment five ivory. Dorsum variegated.



Figs. 9–18. Figs. 9–13. *A. peruensis*. 9. Posterior margin of last abdominal tergum, dorsal view. 10. Same, caudal view. 11. Left paramere, dorsal view. 12. Same, caudomesial view. 13. Right pygophoral appendage, ventral view. Figs. 14–18. *A. rolstoni*. 14. Posterior margin of last abdominal tergum, dorsal view. 15. Same, caudal view. 16. Left paramere, dorsal view. 17. Same, caudomesial view. 18. Right pygophoral appendage, ventral view. Symbols: dl, dorsal lobe; ll, lateral lobe; m, membrane; ml, mesial lobe.

Distribution. Brazil (Rio de Janeiro, Paraná, Santa Catarina).

Comment. The holotype was examined.

Antiteuchus peruensis Ruckes, 1964

Figs. 9–13

Antiteuchus (Antiteuchus) peruensis Ruckes, 1961:152 (not described); Ruckes, 1964: 84, 85–86, figs. 3, 47–49.

Diagnosis. Last abdominal tergum with mesial process deflexed and bifid apically (Figs. 9, 10). Head of each paramere trilobed; viewed dorsally, lateral lobe truncate, dorsal lobe thin and curving laterally, mesial lobe divided apically (Fig. 11); viewed caudomesially, divisions of mesial lobe almost at right angles (Fig. 12). Lateral outline of lateral pygophoral appendages sinuous from ventral view (Fig. 13). First and second antennal segments subequal in length, each about one-third length of third; fourth segment piceous, fifth entirely ivory. Dorsum tan to unaided eye with dark discal spot on each corium, not at all variegated.

Distribution. Peru (Huanuco).

Comment. This is one of two species with a bifid tergal process, the other being *A. rolstoni*. The holotype was examined.

Antiteuchus rolstoni Engleman, 1976

Figs. 14–18

Antiteuchus (Antiteuchus) rolstoni Engleman, 1976:533–536, figs. 1–6.

Diagnosis. Last abdominal tergum with mesial process deflexed and bifid apically (Figs. 14, 15). Head of each paramere trilobed; viewed dorsally, lateral lobe subtriangular to arcuate, rounded apically (Fig. 16); both dorsal and mesial lobes convexly cupped; viewed caudomedially, both dorsal and mesial lobes concavely cupped (Fig. 17). Second antennal segment two-thirds length of first, nearly one-third length of third. Color of antennae and dorsum as in preceding species.

Distribution. Colombia (Amazonas); Ecuador (0°26'S, 76°38'W); Napo River (Ecuador or Peru).

Comments. The holotype, one paratype and two other specimens were examined.

***Antiteuchus rufitarsus*, new species**

Figs. 19–22

Diagnosis. Mesial process on posterior margin of last abdominal tergite of male convexly produced. Ventromesial lobe of paramere-head bearing series of carinae on its convex surface. Tarsi rufous.

Description. Flavescent, punctation dark castaneous to black; scutellum clouded by basal and subapical dark infusions; discal spot on each hemelytron fuscous, exocorium rufously infused apically; tarsi rufous.

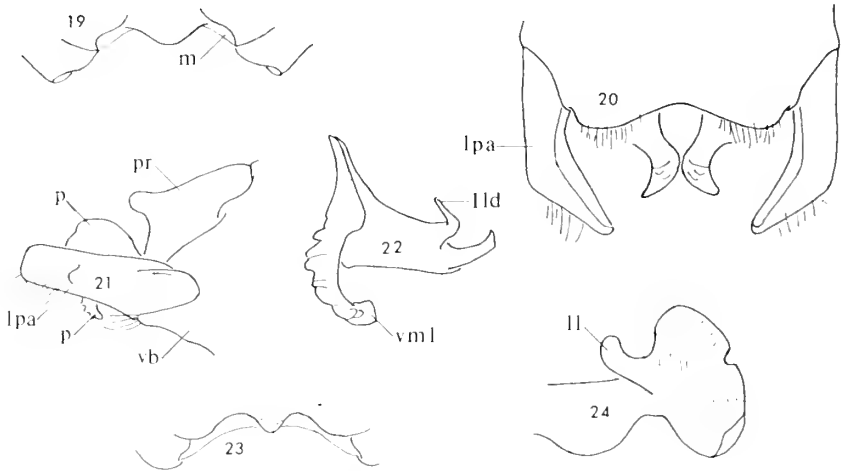
Head. Lateral jugal margins somewhat reflexed; narrow, black border evanescent toward apex of each. Post-clypeus and vertex outlined by black, punctate line; similarly colored and punctate rete on vertex. Punctures on jugs mostly in short, randomly directed lines.

Basal three segments of each antenna largely fuscous on inferior surface, largely flavescent on superior surface, with some spotting on mesial surface, and complete annulus on distal one-fourth of third segment; fourth segment flavescent, infuscated as annulus on middle one-third of segment; fifth segment missing. Antennal setae very short.

Venter of head irregularly punctate. Apex of rostrum reaching anterior margin of fifth abdominal sternite.

Thorax. Anterolateral margins straight, narrowly reflexed outside of submarginal line of punctures; well defined collar on anterior margin behind interocular part of head. Most punctures connected by castaneous to black suffusions from punctures into short, more or less transverse lines.

Scutellar punctation similar to that of pronotum; basal disk and tongue vaguely maculated by extensive suffusions from punctures. Corium of each hemelytron thickly, irregularly punctate. Discal macule at end of R+M vein large, fuscous, entirely on endocorium; exocorium with rufous infusion apically and numerous flavescent or rufous calli scattered along its length; apical angle of corium reaching or nearly



Figs. 19–24. Figs. 19–22. *A. rufitarsus*. 19. Posterior margin of last abdominal segment, dorsal view. 20. Posterior portion of pygophore, ventral view. 21. Same, lateral view. 22. Right paramere, caudal view. Figs. 23, 24. *A. bartletti*. 23. Posterior margin of last abdominal segment, dorsal view. 24. Left paramere, excised. Symbols: ll, lateral lobe; lld, lateral lobe, dorsal branch; lpa, lateral pygophoral appendage; p, paramere; pr, protiger; m, membrane; vb, ventral border; vml, ventromesial lobe.

reaching abdominal apex. Boundary between corium and membrane diagonal, slightly sinuous; membrane moderately fumose basally, becoming lighter toward margin, with 7 veins.

Thoracic pleura rather thickly and uniformly punctate, impunctate evaporative areas excepted. Ivory callus on posterior margin of each mesopleuron removed from lateral margin by distance subequal to length of callus; ivory callus on lateral margin of metapleuron not reaching posterior margin. Punctuation posterior to evaporative area of metapleuron not black, similar to thoracic punctuation elsewhere. Ostiolar ruga reaching one-half of distance from ostiole to lateral margin of metapleuron, with step-down about one-fourth of this distance and evanescing beyond step-down.

Numerous fuscous spots on femora, some on tibiae, suggestion of one subbasal and one subapical annulus on each hind tibia; setae on legs short excepting apical tuft of long setae on mesial surfaces of hind tibiae and scattered setae on third tarsal segments; tarsi bright rufous.

Abdomen. Connexiva alternated; large black macule at each incisure contrasting strongly with intervening flavescent border.

Punctuation of venter shallow, rufous, dense along margins, diminishing in density toward meson. Spiracles black, oval. Lateral margins of venter narrowly black-bordered on each side of incisures. Mesial sulcus broad, shallow, extending from base of abdomen to last sternite. Process on posterior margin of last tergite convex; entire tergal margin trisinate; membrane reduced (Fig. 19).

Genitalia. Lateral apical appendages of pygophore about 3.5 times as long as basal width, bent mesad subapically (Fig. 20); mesial face of each flat or slightly convex;

dorsolateral surface distad of bend bearing elongated black macule. Posteroventral margin of pygophore produced, concavely emarginate, fringed with long hair, most densely so laterally. Apical lobes of proctiger semi-erect (Fig. 21). Parameres essentially bipartite with foliar mesial part and lateral, bifid lobe; dorsomesial lobe laminate, subvertical, concave mesially, continuing ventrad as ventromesial lobe; ventromesial lobe curled laterad and entad, bearing on its convex surface about 6 parallel carinae; lateral lobe of each paramere divided into dorsal and ventral processes, both curved and apically acute (Fig. 22).

Female unknown.

Measurements (mm). Head 3.5 wide, 2.4 long; interocular width 1.95, between ocelli 0.95, across ocelli 1.25, from each ocellus to nearest eye 0.40. Length of segments 1–4 of antennae (5th missing) 0.8; 1.05; 2.00; 3.05. Length of segments 1–4 of rostrum 1.10; 2.25; 1.70; 1.10. Pronotal width 6.8, mesial length 2.9. Scutellar width 4.6 at base, length 6.0. Body length without membranes 10.4.

Type. Holotype, male labeled "VENEZUELA: T. F. Amaz. Cerro de Neblina Base Camp. 140 M. 0°50'N. 66°9'W. 24 Nov–1 Dec., 1984. R. L. Brown." Deposited in the Natural History Museum, London. No paratypes.

Comments. The convex tergal process relates this species to *A. bartletti* Ruckes, from which it is distinguished by the carinate ventromesial lobe of the parameres. Carinae on the paramere-heads are also present in *A. ruckesi* Rolston and *A. englemanni*, new species; neither of these species has a convex tergal process.

Etymology. Named for the conspicuously rufous tarsi.

Antiteuchus bartletti Ruckes, 1964

Figs. 23–24

Antiteuchus (Antiteuchus) bartletti Ruckes, 1964:85, 97–98, Figs. 72–74.

Diagnosis. Last abdominal tergum with convex, entire, mesial process; membrane extending entirely across posterior tergal margin between tergal process and connexival sclerites (Fig. 23). Parameres without carinae, each with large, bicurved, mesial lobe and small, hooked, lateral lobe (Fig. 24). Second antennal segment four-tenths length of third (sec. Ruckes, 1964). Tarsi brownish yellow.

Distribution. Guyana.

Comment. The paratype was examined. Ruckes (1964) noted that both the holotype and paratype were mutilated.

Antiteuchus amplus (Walker, 1867)

Figs. 25–27

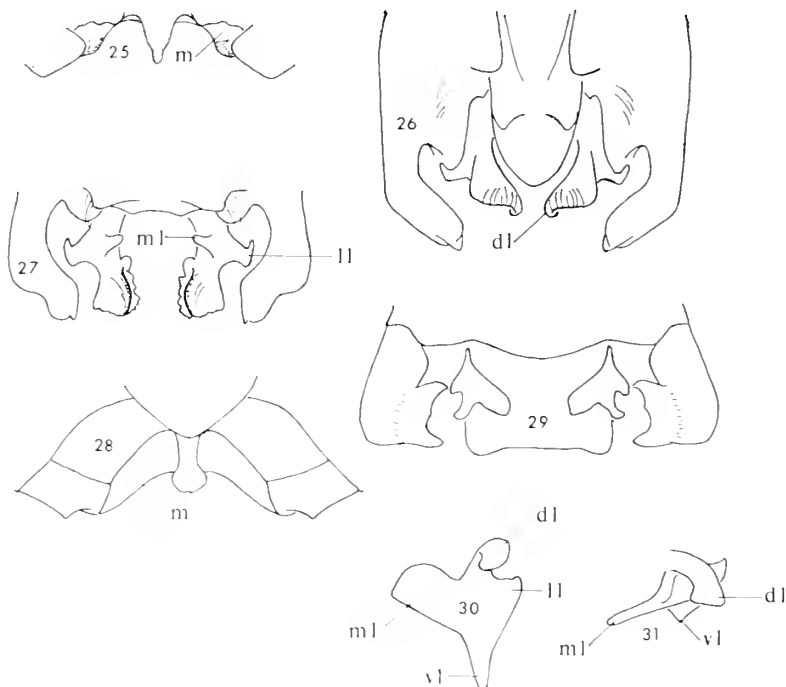
Discocephala ampla Walker, 1867:187–188.

Dinocoris ampla: Distant, 1899:444.

Mecistorhinus amplus: Kirkaldy, 1909:218; Costa-Lima, 1940:54.

Antiteuchus (Antiteuchus) amplus: Ruckes, 1964:84, 86–87, figs. 42–44 (keyed, described).

Diagnosis. Mesial process of last abdominal tergum papilliform (Fig. 25); membrane on each side of tergal process nearly partitioned, incorporating sclerite near connexival sclerite. Head of each paramere trilobed, dorsal lobe with parallel carinae



Figs. 25-31. Figs. 25-27. *A. amplus*. 25. Posterior margin of last abdominal segment, dorsal view. 26. Posterior portion of pygophore, dorsal view. 27. Same, caudoventral view. Figs. 28-31. *A. cuspidatus*. 28. Last abdominal segment, dorsal view. 29. Posterior portion of pygophore, caudoventral view. 30. Right paramere-head, caudal view. 31. Same, dorsal view. Symbols: dl, dorsal lobe; ll, lateral lobe; m, membrane; ml, mesial lobe; vl, ventral lobe.

(Figs. 26, 27). Third antennal segment twice length of second; basal fourth of segment four, basal half and apical tenth of segment five sordid ivory, remainder of these segments fuscous. Dorsum variegated.

Distribution. Brazil (Amazonas); Peru (tributaries of Amazon River).

Comment. A specimen determined by Ruckes was examined.

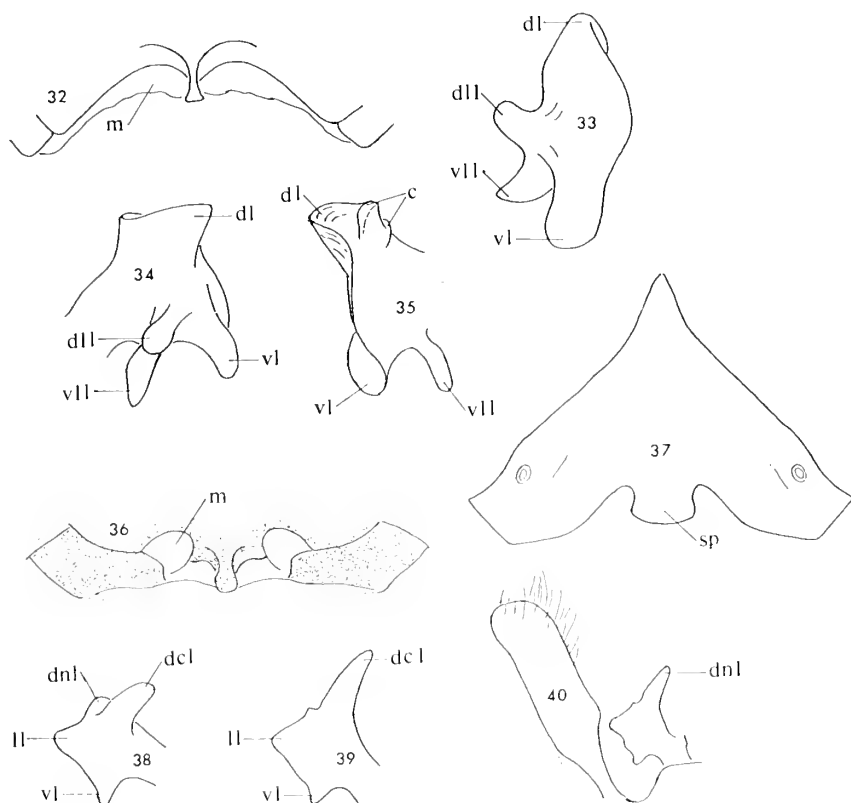
Antiteuchus cuspidatus Ruckes, 1964

Figs. 28-31

Antiteuchus (Antiteuchus) cuspidatus Ruckes, 1964:85, 98-100, figs. 69-71.

Diagnosis. Lateral pygophoral appendages with pincer-shaped process on mesial face of each (Fig. 29). Mesial process of last abdominal tergum elongated, sides subparallel, apex expanded, rounded and slightly notched mesially (Fig. 28). Each paramere head with four lobes (Figs. 30, 31). Second antennal segment about four-tenths length of third; pale, narrow, subbasal annulus on fourth segment sometimes obscure, basal half of fifth ivory. Dorsum variegated.

Distribution. Colombia (Cundinamarca); Panama (Canal Zone).



Figs. 32–40. Figs. 32–35. *A. tessalatus*. 32. Posterior margin of last abdominal segment, dorsal view (after Ruckes, 1964). 33. Left paramere, caudal view. 34. Same, dorsolateral view. 35. Same, ventromesial view. Figs. 36–40. *A. geometricus*. 36. Posterior margin of last abdominal segment, dorsal view. 37. Last abdominal sternite. 38. Head of left paramere, caudal view. 39. Same, ventral view. 40. Left lateral phygophoral appendage and paramere, ventral view. Symbols: c, carina; dcl, dorsoectal lobe; dl, dorsal lobe; dll, dorsolateral lobe; dnl, dorsoentol lobe; ll, lateral lobe; m, membrane; sp, sternal process; vl, ventral lobe; vll, ventrolateral lobe.

Comment. Three specimens from Panama determined by Engleman were examined. These were collected from a canopy of *Luehea seemanii* Tr. and Pl., family Tiliaceae.

Antiteuchus tessalatus (Westwood, 1837)

Figs. 32–35

Dinidor tessalatus Westwood, 1837:24–25.

Macrothyreus annulicornis Fieber, 1851:458. (synonymized by Ruckes, 1964)

Dinocoris tessalatus: Stål, 1872:9.

Dinocoris tessallatus [sic]: Lethierry & Severin, 1893:86.

Dinocoris tesselatus [sic]: Distant, 1901:808.

Mecistorhinus tessalatus: Kirkaldy, 1909:218.

Grimgerda annulicornis: Kirkaldy, 1909:218.

Antiteuchus (Antiteuchus) annulicornis: Ruckes, 1961:152 (listed).

Antiteuchus (Antiteuchus) tessalatus: Ruckes, 1961:152 (listed); Ruckes, 1964:84, 88–89, figs. 50–52 (keycd, description).

Diagnosis. Mesial process of last abdominal tergum expanded apically, truncate, entire, its sides concave from dorsal view (Fig. 32). Each paramere-head with four lobes; dorsal and ventral lobes lamellar, each rolled into scoop-shaped curve (Figs. 33–35); dorsal lobe bearing short, low carina visible from ventromesial aspect (Fig. 35). Second antennal segment about one-third length of third; fourth and fifth segments fuscous, each with broad, pale annulus basally. Dorsum variegated.

Distribution. Brazil (Rio de Janeiro); Guyana.

Comments. The holotype and one other specimen was examined. The holotype now lacks the tergal process, and the right paramere has been removed and glued into the pygophore upside down.

Antiteuchus geometricus Engleman, 1983

Figs. 36–40

Antiteuchus (Antiteuchus) geometricus Engleman, 1983:188, figs. 14, 18, 19.

Diagnosis. Last abdominal sternite with mesial, subquadrate process on posterior margin (Fig. 37). Tergal process elongate, apically expanded and entire; posterior margin of last abdominal tergum deeply, complexly emarginate on each side of tergal process (Fig. 36). Head of each paramere four lobed, large dorsoectal lobe projecting posteriorly (Figs. 38–40). Viewed ventrally, mesial margin of each lateral pygophoral appendage projecting obtusely toward lateral lobe of corresponding paramere (Fig. 40). Second antennal segment about half as long as third; basal annulus on segment four, basal third and tip of five, pale.

Distribution. Brazil (Amazonas).

Comments. The holotype was examined.

This is the only *Antiteuchus* species with a mesial process on the posterior margin of the last abdominal sternite.

Antiteuchus englemani, new species

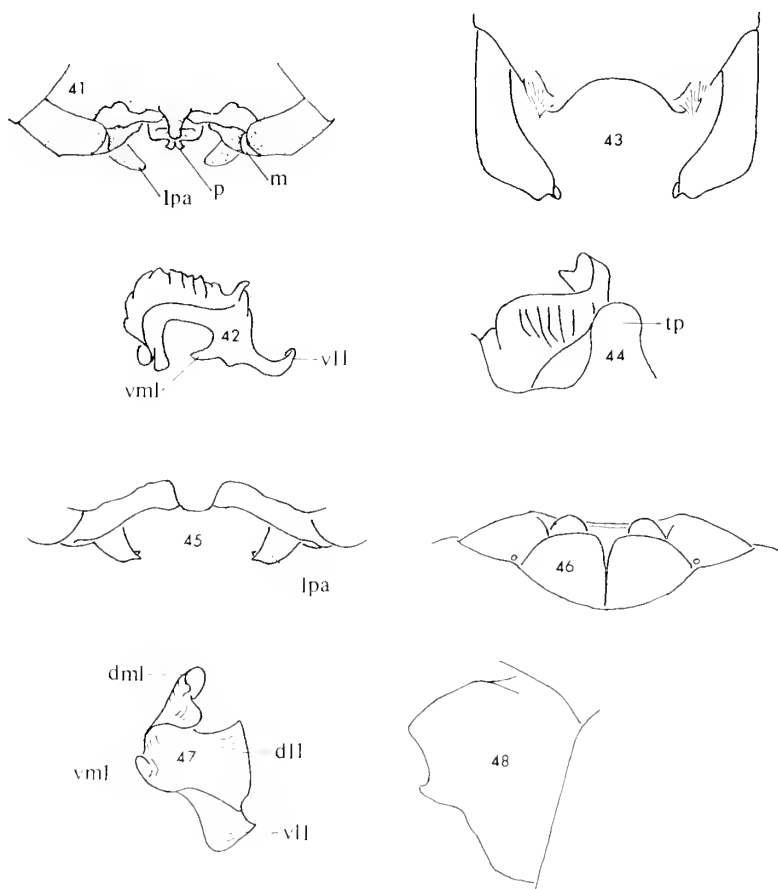
Figs. 41–44

Diagnosis. Tergal process papilliform from dorsal view, actually depressed, reflexed apically; tergal emargination deep, strongly sinuous (Fig. 41); membrane enclosing a pair of sclerites. Dorsal lobe of each paramere-head bearing carinae (Fig. 42).

Description. Flavescent, heavily marked dorsally with castaneous to black punctures, vermiform lines, retes and macules.

Head. Lateral jugal margins reflexed just before anteocular concavities; black edging extending from eyes toward apex, evanescent toward apex. Clypeus broadly black bordered except basally. Vertex outlined and covered by black, punctate rete. Punctures of jugal surface black, most in short lines and small clusters.

First, second and basal 0.5–0.6 of third antennal segments heavily spotted and daubed with black, anterior surface of these segments nearly solid black; basal 0.3



Figs. 41–48. Figs. 41–44. *A. englemani*. 41. Posterior margin of last abdominal segment and part of pygophore, dorsal view. 42. Right paramere, dorsocaudal view. 43. Posterior portion of pygophore, ventrocaudal view. 44. Tergal process and right paramere, dorsal view. Figs. 45–48. *A. pallesceus*. 45. Posterior margin of last abdominal segment and part of pygophore, dorsal view. 46. Genital plates, caudoventral view. 47. Right paramere, caudal and slightly mesial point of view. 48. Right lateral pygophoral appendage, caudal view. Symbols: dml, dorsomesial lobe; dll, dosolateral lobe; lpa, lateral pygophoral appendage; m, membrane; p, paramere; tp, tergal process; vll, ventrolateral lobe; vml, ventromesial lobe.

of fourth segment, basal 0.4 and apical 0.15 of fifth segment flavescent, remainder of last two segments black. Setae on all segments shorter than diameter of supporting segment. Rostral apex reaching posterior margin of sixth abdominal sternite.

Thorax. Anterolateral pronotal margins straight, each narrowly reflexed outside black, punctate, submarginal line; collar weakly to moderately defined; most punctures other than those in submarginal lines connected by short, generally transverse, dark lines, these forming rete on posterior pronotal disk.

Most scutellar punctures connected into fuscous to black vermiform lines, these aggregated into incomplete, large macule on basal disk and longitudinal, post-frenal pair of vague macules.

Endocorium of each hemelytron with large, fuscous macule at end of R+M vein, punctation other than in macule similar to that on scutellum; punctures on clavus bright castaneous, discrete; those on exocorium also castaneous, mostly aggregated in short lines or small clusters. Costal angle of each corium nearly reaching abdominal apex; margin joining membrane slightly sinuous. Membrane moderately fumose basally, becoming lightly fumose distally; veins simple, 6 or 7 in number.

Thoracic pleura rather uniformly punctate excepting impunctate evaporative areas; propleura somewhat more densely punctate than mesopleura; punctures caudad of evaporative areas black, elsewhere dark castaneous. Callus located on posterior margin of each mesopleuron submarginal to lateral margin; each callus on metapleuron in posterolateral angle but slightly separated from posterior margin; all calli ivory. Each ostiolar ruga evanescent distally, extending 0.33–0.45 of distance from mesial limit of ostiole to lateral margin of metapleuron, with step-down at 0.25 of this distance. Femora and sulcate surface of tibiae with many small, dark spots; vague, incomplete subapical and subbasal ring present on all tibiae; setae on legs short excepting long, apical tuft on posterior face of hind tibiae and long, scattered, tarsal setae, especially on third segment.

Abdomen. Connexiva partially exposed; each transverse connexival suture dividing large, black, triangular macule with apex directed mesad.

Density of punctures on sides of venter similar to thoracic punctation, becoming increasingly sparse toward meson; punctures weak, light castaneous. Spiracles black, ovoid. Lateral margins narrowly black-bordered on both sides of incisures. Disk concave basally, third and fourth sternites with broad, shallow sulcus mesially. Posterior margin of last tergum trisinuately emarginate on each side of tergal process, lateral concavity extending around posteromesial angle of last connexival segment; membrane with triangular, black sclerite appearing as continuation of connexivium, this sclerite folded, continuing depression created by connexival suture (Fig. 41). Tergal process as long as wide at posterior margin of membrane, deflexed; apex reflexed, entire, not expanded.

Genitalia. Lateral apical lobes of pygophore curving mesad; inner face flat to slightly concave, outer surface carinate apically. Posteroventral pygophoral margin produced into pair of triangular projections, each just mesad of lateral apical appendage; tuft of setae arising from ventrolateral lateral surface of each projection (Fig. 43). Proctiger mesially carinate, pair of apical lobes directed posteriorly. Parameres contiguous over very apex of proctiger, partially beneath apex of tergal process; each paramere with large, dorsal lobe and two ventral lobes, dorsal lobe shaped as inverted cup, convex dorsal and mesodorsal surfaces bearing about 9 carinae, those on mesoventral surface short, tooth-like; ventrolateral lobe flat, sigmoid from caudodorsal view; ventromesial lobe short, black, flat, narrowly rounded apically (Fig. 42).

Female unknown.

Measurements (mm). Head 3.4–3.35 wide, 2.4–2.35 long; interocular width 1.80, between ocelli 0.90–0.95, across ocelli 1.15, from ocellus to nearest eye 0.35. Length of segments 1–5 of antennae 0.80–0.85; 1.05–1.10; 2.00–2.15; 2.60; 2.65. Length of segments 1–4 of rostrum 1.0–1.05; 2.10–2.30; 1.55; 1.10–1.20. Pronotal width 6.7–

6.9, length 2.8–3.0. Scutellar width 4.4–4.7 at base, 6.0–6.4 long. Body length excluding membranes 11.0–11.3.

Types. Holotype: male labeled (a) ECUADOR; Napo, Coca. 250 M. iii-iv-1982. G. Onore (b) Amazonian rain forest (c) Brit. Mus. 1982-246. Deposited in the Natural History Museum, London. Paratype: male with same labeling as holotype. Scutellum broken.

Etymology. Named for H. Dodge Engleman, M.D. whose entomological endeavors include a substantial contribution to our knowledge of this genus.

Antiteuchis pallescens Stål, 1868

Figs. 45–48

Antiteuchus pallescens Stål, 1868:18.

Antiteuchus (Antiteuchus) pallescens: Ruckes, 1964: 101 (description).

Diagnosis. Tergal process about as long as wide subapically, entire and truncate apically (Fig. 45); posterior margin of last abdominal tergum slightly sinuous on each side of tergal process; membrane extending onto connexival sclerite on each side. Paramere-head four-lobed; dorsomesial and ventromesial lobes curving ectally, dorsolateral lobe curving entally, ventrolateral lobe more or less right angular to other lobes and with ventromesial face concave; dorsomesial lobe divided apically with ventral part more strongly curved than dorsal part (Fig. 47). Lateral pygophoral appendages toothed subapically (Fig. 48). Second antennal segment about half length of third; fourth segment fuscous, fifth (see Ruckes, 1964) broadly ivory at base. Dorsum variegated.

Types. *Antiteuchus pallescens* Stål was based on three of six specimens standing under the name *Edessa sepulcralis* Fabricius, 1803. Ruckes (1964) examined these specimens but did not designate a lectotype. The following designations are made here: male lectotype and 2 female paralectotypes. All three specimens bear a small (ca. 2 cm), square, green card; beneath the green card on the lectotype and on one of the paralectotypes is a white card of similar size and shape bearing the appropriate sex symbol; then on all specimens "TYPE" printed on a red label, followed by a white label with "palecscens Stal" written in green ink. The lectotype is missing both hind legs, the last segment of the left antenna and all of the right antenna except the basal segment. The paralectotype without the small, white card has both hind legs complete, the basal three segments of the right antenna, and the basal four segments of the left antenna. All other appendages except the right metacoxa are missing, and there is a pin-hole in the right basal disk of the pronotum. The other paralectotype lacks the right hemelytron, the last two segments of both antennae, all legs except the left front leg. The genital plates of a paralectotype are illustrated in Figure 46.

The remaining 3 specimens of the series constitute the type material of *Edessa sepulcralis* Fabricius (= *Antiteuchus sepulcralis*), which belongs to the *parallela* species-group of *Antiteuchus*. The following designations are made here: male lectotype, and 1 male and 1 female paralectotypes. All 3 specimens bear a small (ca. 2 cm), square, green card; beneath the green card on the lectotype and female paralectotype is a white card of similar size and shape bearing the appropriate sex symbol; then on all specimens "TYPE" printed on a red label. The lectotype also bears Fabricius's label "Amer. mer., Schmidt; Mus. de Sch-stedt, Edessa sepulcralis, Fabr." The num-

ber "3" is in the lower, left corner. The lectotype lacks both front legs, the left hind leg, and the last segment of the right antenna and last two segments of the left antenna. The female paralectotype has most of the scutellum, basal three terga and basal, ventral disk of the abdomen destroyed; the right hind leg and right antenna are missing, as is the terminal segment of the left antenna. The male paralectotype lacks the last segment of the right antenna and the last two segments of the left antenna.

An appropriate lectotype or paralectotype label has been attached to each specimen, all of which are conserved in the Fabrician collection in the Zoological Museum, Copenhagen, Denmark.

Distribution. "South America": Brazil (Amazonas).

Antiteuchus supinatus Engleman, 1983

Antiteuchus (Antiteuchus) supinatus Engleman, 1983:187–188, figs. 16, 21.

Diagnosis. Posterior margin of last abdominal tergum arcuately emarginate with quadrate, apically entire, mesial process on posterior margin; membrane continuous on each side from subapex of tergal process to connexival sclerite. Lateral pygophoral appendages truncate apically, unarmed. Head of each paramere three-lobed. Second antennal segment about four-tenths length of third.

Distribution. Guyana.

Comments. This species is known only from the holotype, which lacks the last two antennal segments. The holotype was examined nearly a decade ago, but I made no drawings of it.

This species and the similar *A. pallescens* are readily separated by the shape of the lateral pygophoral appendages and differences in the parameres.

Antiteuchus confinium Ruckes, 1964

Figs. 49–51

Antiteuchus (Antiteuchus) confinium Ruckes, 1964:85, 94–95; figs. 63–65.

Diagnosis. Posterior margin of last abdominal tergum arcuately emarginate with elongated mesial process neither expanded, restricted, nor bifid apically (Fig. 49); border of this tergum with crescent-shaped impression extending between lateral pygophoral appendages when viewed from above; membrane extending on each side from subapex of tergal process to connexival sclerites. Head of each paramere three-lobed, lateral lobe acutely angled dorsally (Figs. 50, 51). Second antennal segment about four-tenths length of third; antennae fuscous with last segment of each castaneous distally. Dorsum dark castaneous without notable variegation but with many microscopic, ivory flecks.

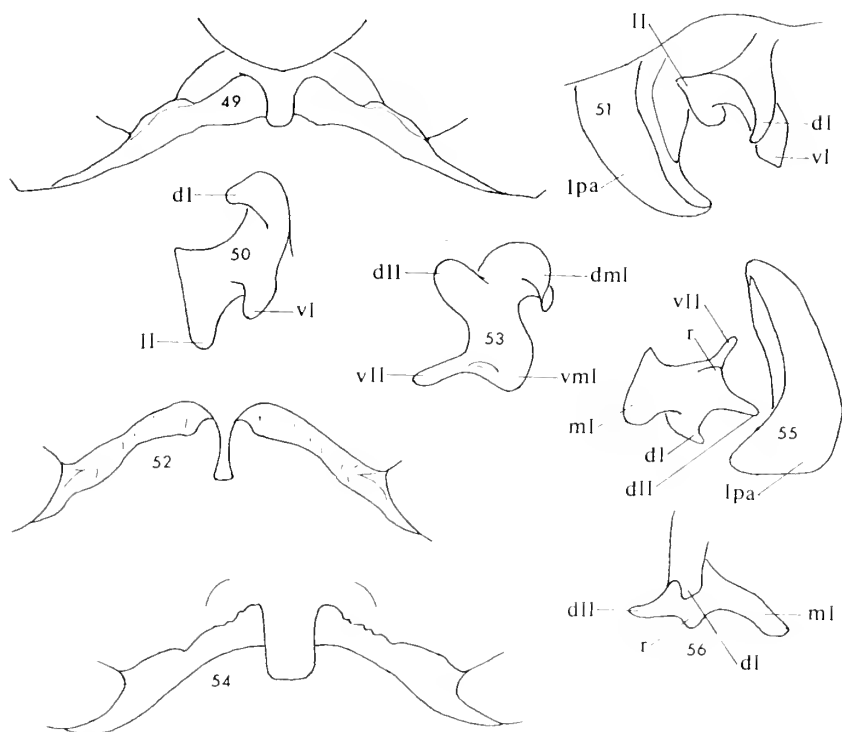
Distribution. Peru-Brazil frontier; Ecuador (Napo).

Comment. Two specimens were examined, one a paratype.

Antiteuchus rideri, new species

Figs. 66–71

Diagnosis. Mesial process of last abdominal tergum subrectangular distad of curving basal expansion, longer than subapical width, apically entire and truncate; emar-



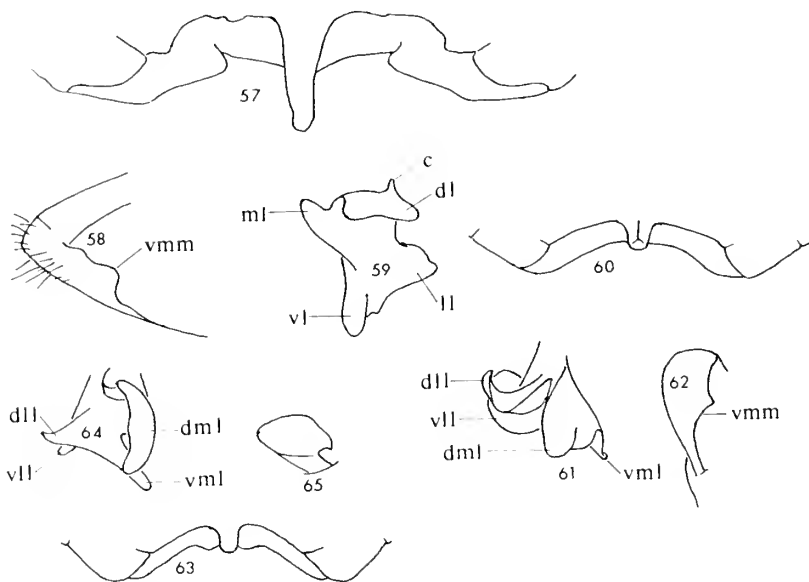
Figs. 49–56. Figs. 49–51. *A. confinium*. 49. Posterior margin of last abdominal segment, dorsocaudal view. 50. Left paramere, caudal view. 51. Left paramere and lateral pygophoral appendage, dorsal view. Figs. 52, 53. *A. marmoratus*. 52. Posterior margin of last abdominal segment, dorsocaudal view. 53. Left paramere, caudal view. Figs. 54–56. *A. guianensis*. 54. Posterior margin of last abdominal segment, dorsocaudal view. 55. Left paramere and lateral pygophoral appendage, caudoventral view. 56. Left paramere, dorsal view. Symbols: dl, dorsal lobe; dll, dorsolateral lobe; dml, dorsomesial lobe; ll, lateral lobe; lpa, lateral pygophoral appendage; ml, mesial lobe; r, rectilinear lobe; vl, ventral lobe; vll, ventrolateral lobe; vml, ventromesial lobe.

gination of last abdominal tergite arcuate on each side of tergal process, not extending cephalad beyond base of process. Head of each paramere trilobed, with two lateral lobes appearing to fuse basally into carina.

Description. Dorsal punctation fine, rather dense; dark brown suffusion around each puncture uniting most punctures into vermiform lines with more or less transverse orientation; lines may be so broad as to obscure most of flavescent background. Coria lack definite discal marks.

Head. Lateral jugal margins very slightly reflexed; narrow, black border may evanesce toward apex. Post-clypeus and vertex defined by line of black punctures; short, vermiform lines on head with confused orientation.

Basal segment of antennae bearing numerous dark spots which may be discrete,



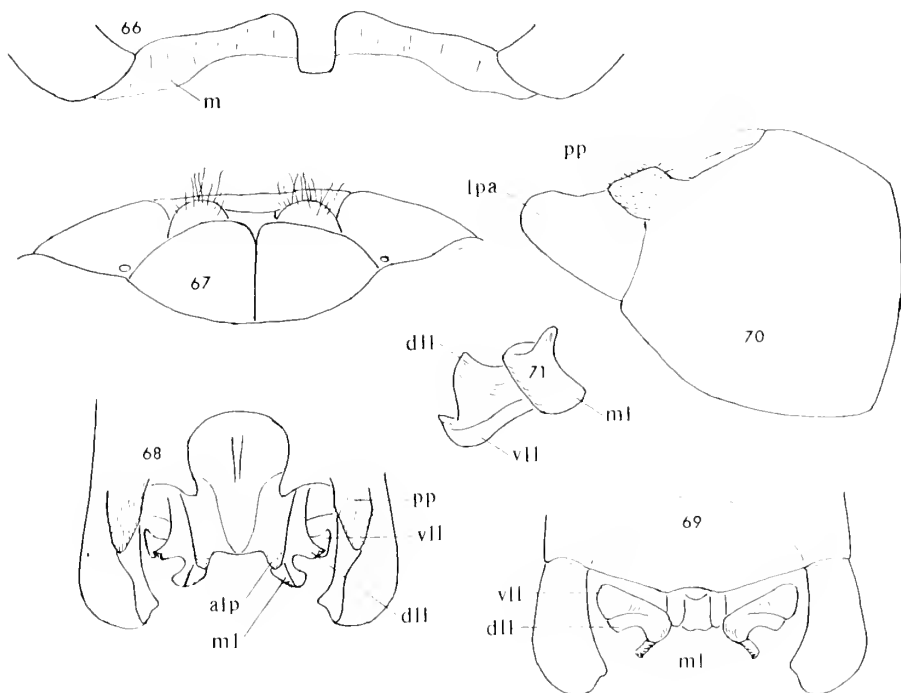
Figs. 57-65. Figs. 57-59. *A. punctissimus*. 57. Posterior margin of last abdominal segment, dorsal view. 58. Apical portion of left lateral pygophoral appendage, caudomesial view. 59. Head of right paramere, caudal view. Figs. 60-62. *A. varians*. 60. Posterior margin of last abdominal segment, dorsal view. 61. Head of left paramere, dorsal view. 62. Ventral surface of left lateral pygophoral appendage, caudomesoventral view. Figs. 63-65. *A. mimeticus*. 63. Posterior margin of last abdominal segment, dorsal view. 64. Head of left paramere, dorsal view. 65. Left lateral pygophoral appendage, caudal view. Symbols: c, carina; dl, dorsal lobe; dll, dorsolateral lobe; dml, dorsomesial lobe; ll, lateral lobe; ml, mesial lobe; vl, ventral lobe; vll, ventrolateral lobe; vml, ventromesial lobe; vmm, ventromesial margin.

or fused into irregular macules covering most of segment; second and third segments entirely fuscous or with lateral surface flavescent for entire length of second and basal one-half of third; basal one-fourth of fourth segment and basal one-half of last segment pale, remainder of fourth segment fuscous, remainder of fifth segment moderately infusate. Antennal setae short.

Venter of head irregularly fuscous punctate. Apex of rostrum reaching fourth or fifth abdominal sternites.

Thorax. Anterolateral margins slightly convex, narrowly reflexed outside of submarginal line of punctures; anterior margin with collar behind interocular part of head. Disk shallowly impressed at posterolateral limit of each cicatrice. Most punctures connected by vermiform, dark lines; orientation of lines predominately transverse.

Scutellar punctation similar to that of pronotum; small, impunctate, mesial macule present basally. Corium of each hemelytron thickly punctate, suffusion from punctures varying among individuals from a few vermiform lines to almost solid covering; apex of corium lying above last tergum; junction between corium and membrane diagonal, corium slightly convex; membrane fumose, with 6 or 7 veins.



Figs. 66–71. *A. rideri*. 66. Posterior margin of last abdominal segment, dorsal view. 67. Genital plates. 68. Posterior portion of pygophore, dorsal view. 69. Same, ventral view. 70. Pygophore, lateral view. 71. Left paramere, caudal view. Symbols: alp, apical lobe of proctiger; dll, dorsolateral lobe; lpa, lateral pygophoral appendage; m, membrane; ml, mesial lobe; p, paramere; pp, pygophoral process; vll, ventrolateral lobe.

Thoracic pleura thickly and rather uniformly punctate, excepting impunctate, finely wrinkled evaporative areas. Triangular callus in posterolateral corner of each metapleuron ivory. Punctuation posterior to evaporative areas black. Ostiolar ruga reaching one-fourth of distance from ostiole to lateral margin of metapleuron as substantial ridge, there stepped-down and continuing weakly for an equal distance before evanescent.

Femora and tibiae thickly fuscous-spotted, at least on superior surface; setae of legs short except on third tarsal segment; tarsi concolorous with tibiae.

Abdomen. Connexiva weakly alternated, black punctuation and suffusion along transverse sutures forming narrow, imprecise band.

Punctuation of venter shallow, dense laterally, diminishing in density toward impunctate meson; color of punctures and surrounding suffusions darker than background with degree of contrast varying among individuals. Spiracles black, ovoid. Lateral margins of venter very narrowly black-bordered. Mesial sulcus broad, shallow, extending from base of abdomen to last sternite. Process on posterior margin of last tergite subrectangular beyond point where sides of process curve laterad into posterior tergal margin (Fig. 66); apex of process entire, truncate, curving ventrad. Membrane

reaching apically on process to point where process curves ventrad, extending uninterruptedly on each side to connexival sclerite.

Genitalia. Lateral apical appendages of pygophore nearly three times as long as wide at base, measured ventrally; mesial face of appendages quite concave, dorsal surface with large impressed area about midway between base and apex; ventromesial edge bearing large, blunt tooth subapically (Figs. 68, 69). Posteroventral margin of pygophore convexly produced, mesially truncate; ventral surface between appendages slightly impressed, sparsely clothed with long hairs; dorsolateral margins each produced above appendage into posteriorly directed, compressed process thickly covered by short hairs, its posterior margin sloping ventrad (Fig. 70). Apical lobes of proctiger nearly horizontal. Head of each paramere trilobed; mesial lobe broad, thin, projecting ectad, apically recurved and truncate (Fig. 71); lateral lobes appear fused basally, their joint carinate, both lobes broad, thin; dorsolateral lobe subvertical, recurved; ventrolateral lobe with concave posteroventral surface, apically recurved.

Punctuation of basal plates moderately and uniformly dense, shallow, rufous; posterior margins evenly arcuate. Ninth paratergites little exposed, bearing numerous long setae. Spiracle conspicuous on each of eighth paratergites (Fig. 67).

Measurements (mm). Head 3.25–3.5 wide, 2.3–2.4 long; interocular width 1.85–2.0, between ocelli 0.9–1.0, across ocelli 1.15–1.25, from each ocellus to nearest eye 0.4. Length of segments 1–5 of antennae 0.8; 0.8–0.9; 1.8–2.0; 2.3; 2.3. Length of segments 1–4 of rostrum 1.0–1.1; 2.0; 1.4–1.6; 0.9–1.0. Pronotal width 6.5–6.9, mesial length 2.8–2.9. Scutellar width 4.5–4.8 at base, length 5.9–6.1. Body length without membranes 9.8–11.7.

Types. Holotype, male, labeled “Santarem, July 1919. S. M. Klages. Acc. 6324.” Deposited in the Natural History Museum, London. Paratypes male and female, both labeled “BRAZIL: PARA: Rio Xingu Camp (52°22'W, 3°39'S) ca 60km S. Altamira 8–12 Oct 1986. P. Spangler & O. Flint.” Deposited in the National Museum of Natural History, Washington, D.C.

The tergal process of the male paratype has the apical part broken off. The mesial lobe of the left paramere is also damaged.

Etymology. Named for my colleague, D. A. Rider, who has contributed much to pentatomid systematics.

Antiteuchus marmoratus (Erichson, 1848)

Figs. 52–53

Cataulax marmoratus Erichson, 1848:609.

Dinocoris (Mecistorhinus) marmoratus: Stål, 1872:8.

Mecistorhinus (Mecistorhinus) marmoratus: Kirkaldy, 1909:217.

Antiteuchus (Antiteuchus) marmoratus: Ruckes, 1961:152; Ruckes, 1964:84, 87–88.

Antiteuchus (Antiteuchus) ratcliffei Engleman, 1983:184, figs. 13, 17. **NEW SYNONYMY.**

Diagnosis. Mesial process on last abdominal tergum digitiform, apically entire, scarcely expanded (Fig. 52); membrane on each side of tergal process extending uninterruptedly along arcuate emargination to connexival sclerite. Head of each paramere with four lobes (Fig. 53); ventrolateral lobe subcylindrical; ventromesial lobe palmate; dorsal lobes compressed, dorsolateral lobe curving entad, dorsomesial

lobe curving ectad. Lateral apical appendages of pygophore relatively short, each about 1.5 times as long as basal width, its mesial face flat. Second antennal segment about four-tenths length of third; basal fourth of segment four pale; base of five sordid ivory (sec Ruckes, 1964).

Distribution. Guyana.

Comments. Although Ruckes (1964) gave a lengthy description of this species, he apparently did not see the holotype. He stated that the holotype was female and that he had not seen a male of the species. The holotype, conserved in the Museum für Naturkunde der Humboldt-Universität zu Berlin, is a male. Misstatement of the holotype's sex discouraged subsequent examination of it because females of this group usually lack characters unique to their species. The type is in good condition but lacks the fifth antennal segments and the last two rostral segments.

Antiteuchus guianensis Ruckes, 1964

Figs. 54–56

Antiteuchus (Antiteuchus) guianensis Ruckes, 1964:85, 95–96, figs. 66–68.

Diagnosis. Last abdominal tergum unevenly and arcuately emarginate with denticulate margin on each side of tergal process (Fig. 54); tergal process longer than subapical width, subrectangular, apically entire and truncate; membrane extending uninterruptedly on each side from tergal process onto connexival sclerite. Each paramere head 5-lobed; mesial lobe largest with acute ventromesial corner (Fig. 56); dorsal lobe next in size, curving posteriorly at apex; both ventrolateral and dorsolateral lobes spinose; small, rectilinear lobe located above ventrolateral lobe, formed at junction of ventral margin of mesial lobe and ventral margin of dorsolateral lobe (r, Fig. 56). Lateral pygophoral appendages hooked mesad, their mesial face flat basically, convex apically, not impressed (Fig. 55). Second antennal segment nearly four-tenths length of third; base of segment four and both base and apex of five sordid ivory (sec Ruckes, 1964). Dorsum somewhat mottled.

Distribution. French Guiana, Guyana.

Comment. The holotype was examined. Unfortunately, it has only one segment of one antenna.

Antiteuchus punctissimus Ruckes, 1964

Figs. 57–59

Antiteuchus (Antiteuchus) punctissimus Ruckes, 1964:84, 92–94, figs. 60–62.

Diagnosis. Last abdominal sternum shallowly, arcuately emarginated. Tergal process long, digitiform, tapering evenly from base to narrowly rounded, entire apex (Fig. 57); membrane extending without interruption on each side from tergal projection onto connexival sclerite. Each paramere head four-lobed; dorsal lobe broad, nearly horizontal, concave ventrally, strongly carinate dorsally (Fig. 58); both lateral and mesial lobes acute apically, former curving entad, latter curving ectad; ventral lobe compressed, oriented more or less at right angles to dorsal lobe. Mesial face of each lateral pyrophoral appendage impressed; ventral margin of impressed area sharp, produced into blade apically (Fig. 59). Second antennal segment one-half length of

third. Dorsum appearing rather uniformly brown to unaided eye, slightly lighter toward scutellar apex.

Distribution. Brazil (Pará).

Comment. The single paratype was examined.

Antiteuchus varians Ruckes, 1964

Figs. 60–62

Antiteuchus (Antiteuchus) varians Ruckes, 1964:85, 91–92, figs. 56–59.

Diagnosis. Arcuate emargination in last abdominal tergite shallow; tergal process subquadrate, tectiform dorsally, entire apically; membrane on each side reaching apex of tergal process, extending laterad onto connexival sclerite (Fig. 60). Head of each paramere four-lobed but with dorsomesial lobe shallowly bifid, curved ectad; ventromesial lobe small, acute apically, curving ectad; dorsolateral lobe as broad as dorsomesial lobe, acutely angulate dorsally, curved entad; ventrolateral lobe wider distally than at base, concave ventrally, its posterior margin continuous with posterior margin of ventromesial lobe (Fig. 61). Mesial face of lateral pygophoral appendages impressed; ventral margin of impression produced subapically as small tooth (Fig. 62). Second antennal segment one-half length of third; segment four black; basal half of five pale, apical half dusky to black. Color of dorsum black to unaided eye in relatively fresh specimens.

Distribution. Guyana; Brazil (Amazonas).

Comments. The holotype was examined.

A single specimen was collected by G. Couturier at Manaus from *Annona muricata* L. (family Annonaceae), a tree with edible fruit that is known locally as "graviola."

Antiteuchus mimeticus Ruckes, 1964

Figs. 63–65

Antiteuchus (Antiteuchus) mimeticus Ruckes, 1964:85, 100–101, figs. 75–77.

Diagnosis. Last abdominal tergum arcuately emarginate; tergal process longer than apical width, sides curved from base to slightly expanded apex; membrane nearly reaching apex of tergal process, widest near this process, extending laterad on each side onto connexival sclerite (Fig. 63). Head of each paramere, four-lobed; dorsomesial lobe largest, vertical, lateral face concave; dorsolateral lobe small, triangular, directed laterad; ventromesial lobe digitiform, parallel sided, rounded apically, directed primarily mesad; ventrolateral lobe diagonally oriented with subacute, ventromesial, apical angle entad to rest of truncate apex (Fig. 64). Each lateral pygophoral appendage obtusely rounded apically, its mesial surface impressed; mesoventral margin produced apically as small tooth (Fig. 65). Second antennal segment four to five-tenths length of third; base of segment four, basal half and apex of five, pale.

Distribution. Peru.

Comment. The holotype was examined.

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The graciousness of several curators permitted me to examine the holotypes of nearly all the species in the *incurvia* species group, and type material or authentically determined specimens

of the remaining species save one. For this privilege I am indebted to N. Møller Andersen (Zoologisk Museum, Copenhagen), J. Deckert (Museum für Naturkunde der Humboldt Universität zu Berlin), Richard C. Froeschner (U.S. National Museum of Natural History), I. Lansbury (University of Oxford), Randall T. Schuh (American Museum of Natural History) and Ana Yoshi Harada (INPA, Manaus).

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**FIRST RECORD OF PHRUDINAE
(HYMENOPTERA: ICHNEUMONIDAE) FROM SOUTH AMERICA
WITH NOTICE OF A NEW GENUS AND
SPECIES FROM CHILE**

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Abstract. — *Notophrudus mendozi*, new genus and species, resembles the Holarctic genus *Phrudus* (as defined by Townes, 1971) but has a tiny though strong tooth dorso-apically on the front tibia, lacks pectination on the tarsal claws and has the 1st gastric segment uniquely slender, parallel-sided, and with its spiracle closer to the tergal base than in any other phrudine. *Notophrudus* inhabits *Nothofagus* forests in Chile's Lake District (Cautín to Osorno Provinces).

The Phrudinae (Townes, 1971) are a small, polythetic subfamily in which the flagellum often is stout, moniliform and with fewer than 20 segments; the clypeal margin has a transverse fringe of long and parallel setae; and the gastric epipleura are wide, decumbent and often not separated by creases from their tergites (or with only epipleura 2 and 3 so demarked). The subfamily occurs in all biogeographic realms with best representation in the Holarctic but with species also in the Neotropic, Neantarctic (temperate Chile and nearby southwest Argentina), Australian, Oriental, and Ethiopian regions. Two of the 10 phrudine genera have been reared and these are endoparasites of coleopterous larvae.

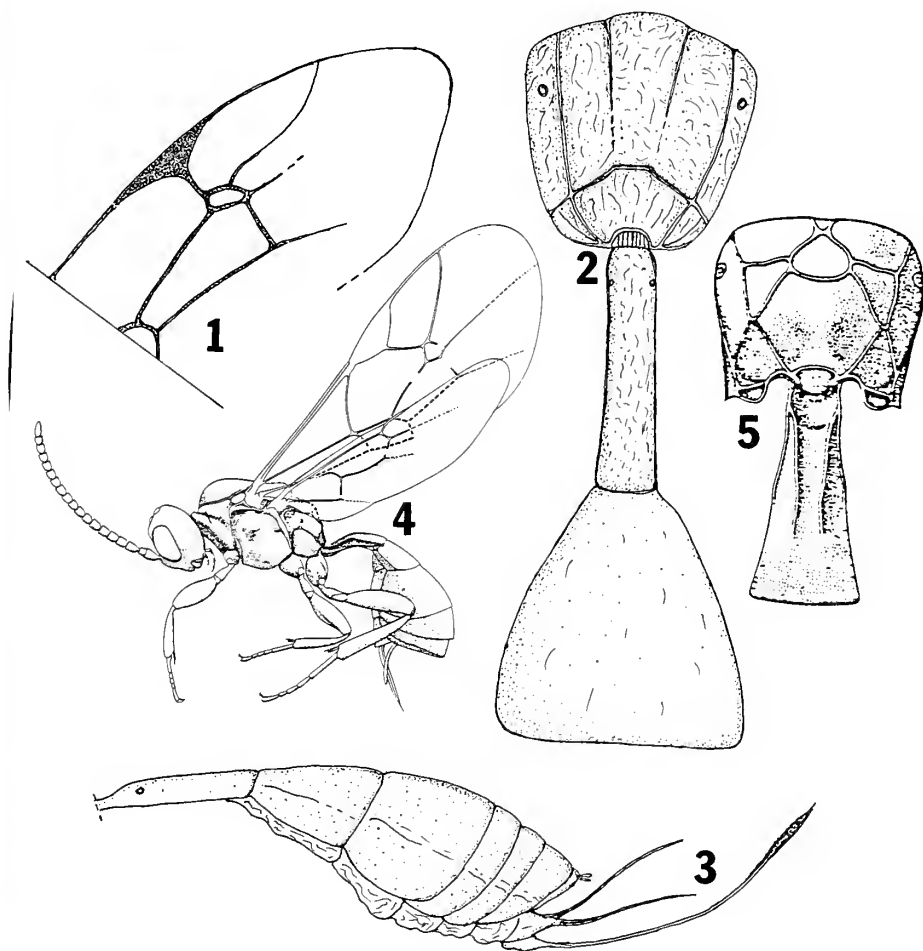
Notophrudus shares many characters with *Phrudus* (Townes, 1971; Gauld, 1984), but differs in such features as its small though strong tooth on the dorso-apical end of the front tibia, its lack of teeth on the tarsal claws, in its scheme of propodeal areolation (cf. Figs. 2 and 5), in its uniquely elongate 1st gastric tergite with spiracles much closer to the base than to the middle (cf. Figs. 3 and 4), in its somewhat compressed gastric tergites 2 and following [the type species of *Phrudus*, *P. monilicornis* Bridgman (1886), has the gaster bulbous and circular in cross section], and by its upcurved ovipositor which is much longer than the apical height of the gaster.

Phrudus Foerster, 1868

Figs. 4-5

Phrudus Foerster, 1869:196. (Type species *Phrudus monilicornis* Bridgman, 1886, by monotypy.)

Townes' (1971) figures of *Phrudus monilicornis* Bridgman are included to facilitate appreciation of the notable differences between this genus and *Notophrudus* Porter, as seen in ovipositor length, gastric proportions and contours, propodeal areolation, and wing venation.



Figs. 1–5. Figs. 1–3. *Notophrudus mendozi*, female. Holotype. 1. Apical half of fore wing showing venation. 2. Dorsal view of propodeum and first 2 gastric tergites. 3. Lateral view of gaster and ovipositor. Figs. 4–5. *Phrudus monilicornis*, female. Type species of *Phrudus*. 4. Entire insect in lateral view (from Townes, 1971). 5. Propodeum and first gastric segment in dorsal view (from Townes, 1971).

Notophrudus, new genus

Figs. 1–3

Diagnosis. Flagellum unusually short; in females 0.7 as long as fore wing, with 16–17 segments of which those in its apical 0.3 are moniliform; in males with 19 flagellomeres, all moniliform. Clypeus 2.4 as wide as long, broadly elliptic, its surface weakly convex and subapically bearing a transverse fringe of numerous (but not dense) long and parallel setae. Temple long and broad, in dorsal view convex and gently receding rearward; 1.1 as long as eye in lateral view. Frons smooth and polished.

Malar space without a vertical suture. Front tibia with a tiny but strong tooth on its apex dorso-apically. Tarsal claws not pectinate. Mesopleuron mostly smooth and shining on its upper 0.5 but ventrally less polished and with fine reticulation; epicnemial carina well developed over its entire extension from the lower part of the mesopleuron dorsad to about the level of the mid-height of the front mesopleural margin. Pterostigma broadly triangular. Propodeum with basal transverse carina absent, areola and basal area confluent to form an elongately rectangular area (median longitudinal carinae partly weak and in places strong), with apical transverse carina very strong, costula absent, lateral longitudinal carinae traceable throughout but not uniformly strong, and with the pleural and submetapleural carinae strong and percurrent. Areolet irregularly pentagonal, broadly sessile dorsally, 2nd intercubitus partly desclerotized and much longer than the 1st intercubitus; cubital and subdiscoidal veins in large part desclerotized but visible to wing apex; mediella desclerotized except near base; radiella, cubitella, discoidella and brachiella either absent or visible toward base and only briefly pigmented. First gastric tergite very long, slender, and parallel-sided, 3.3 as long as wide at apex, its spiracle much closer to base than to middle. Gaster moderately compressed toward the apex. Ovipositor long (0.4 as long as fore wing), gradually but distinctly upcurved between base and apex, nodus very weak, far from apex of the dorsal valves.

Etymology. *Notophrudus* is a latinized conflation of the Greek words *notos* ("south") and *phroudos* ("gone, ruined"), the name that Foerster (1869)—for unknown reasons—bestowed on what has come to be the type genus of its subfamily.

***Notophrudus mendozi*, new species**

Figs. 1–3

Description. Female. Antenna dark brown, becoming blackish toward apex; head, mesosoma, and gaster shining black with mandible and clypeus pale brown, gastric tergites with a dark brown tint, and sternites pale brown; legs dull pale brown.

Length of fore wing 2.5–3.4 mm.

Flagellum with 16–17 segments of which the basal 8 are submoniliform, the following 8–14/15 are more strongly moniliform but still longer than deep, and the last 3 are more crowded and robust than the others (which makes the flagellum weakly clavate). Head arched dorsally well above the eyes, so that the front ocellus is located high up on the vertical interocular line. Mandible elongate, its lower tooth a little shorter than the upper.

Mesoscutum mesally and apically sublustrous with fine aciculo-punctuation but on the lateral lobes contrastingly smooth and shining; notauli weak but visible for ± 0.5 the mesoscutal length. Ventral metapleuron delicately rugoso-aciculate.

Propodeal spiracle very small, not enclosed by a carina.

First gastric tergite almost parallel-sided in dorsal view and with \pm longitudinally biased fine carinae and aciculae. Following tergites very smooth and polished with only a few scattered, tiny punctures and some widely spaced setae; their epipleura broad (especially 3 and following) but not set off by creases dorsad nor reaching so far ventrad as to cover their sternites. Sternites membranous but with some sclerotized areas.

Male. Length of fore wing 3.6 mm.

Flagellum with 19 segments of which the 5th and following are moniliform and a

little longer than deep; whole flagellum very slightly clavate but with the more apical segments discrete and the last segment sharply pointed distally and 3.5 as long as the penult.

Propodeum with its spiracle larger and more clearly enclosed by a carina than in the female.

Epipleura of gastric tergites 3 and following wider than in the female and \pm meeting ventrad over the sternites.

Holotype. Female, Chile (Cautín, Conguillillo, 4-5-II-1988, 1,150 m, L. Masner), in collection of the American Entomological Institute.

Paratypes. 1 female and 5 males, Chile (Cautín, Conguillillo, 4-5-II-1988, 1,150 m, L. Masner; Osorno, Puyehue, 16-II-1988, 1,200 m, L. Masner), in the American Entomological Institute.

Habitat notes. The type series of *Notophrudus mendozi* was trapped in the Andean precordillera between 38–41° South Latitude within the Valdivian Biotic Subprovince of south-central Chile (Porter, 1991). These forested biotopes are dominated in the arboreal stratum by *Nothofagus* spp. (Fagaceae) along with various Myrtaceae, *Eucryphia* (Eucryphiaceae), *Gevuina* (Proteaceae), and *Drimys* (Winteraceae); in the shrub and large herb stratum, by *Desfontainea* (Desfontaineaceae), *Fuchsia* (Onagraceae), *Berberis* (Berberidaceae), *Myrceugenella* (Myrtaceae), *Embothrium* and *Lomatia* (Proteaceae), *Gunnera* (Gunneraceae), and *Chusquea* (Bambusaceae); as well as in the smaller understory layer by *Asteranthera* (Gesneriaceae), *Philesia* (Philesiaceae), *Viola* (Violaceae), *Calceolaria* (Scrophulariaceae), and *Oxalis* (Oxalidaceae). The Valdivian forests at these latitudes have an annual rainfall varying from 1,100–5,000 mm and exist under a cool-temperate thermic regimen, with highs between 12–22°C in summer and winter minima (at low altitude) averaging from 5–10°C with relatively infrequent dips below freezing (Hoffmann, J., 1982).

The humid Valdivian forest seems an appropriate habitat for *Notophrudus*, since Townes (1971) remarks that *Phrudus* is "usually collected by sweeping in woods."

Specific name. This species is named for Ricardo Mendoza M., Technician at the Instituto de Agronomía of the Universidad de Tarapacá (Arica, Chile), in recognition of his expert and good-natured assistance on many collecting trips.

COLLECTIONS

All material seen during this study is deposited in the American Entomological Institute (3005 SW 56th Avenue, Gainesville, Florida 32608, USA).

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**PHYSICAL AND BIOTIC CORRELATES OF POPULATION
FLUCTUATIONS OF DOMINANT SOIL AND LITTER ANT
SPECIES (HYMENOPTERA: FORMICIDAE) IN
BRAZILIAN COCOA PLANTATIONS**

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Abstract.—The relation between weekly patterns of percent occurrence of dominant ant species in litter and soil samples from a Bahian (Brazil) cocoa plantation and climatic factors was examined. No significant lagged correlations were found for the litter dominants, however the soil dominant *Acropyga* cf. *paramaribensis* showed significant lagged correlations with temperature, rainfall and leaf flush, probably in response to increases in the populations of their mutualistic root mealybugs. Population fluctuations of *A. cf. paramaribensis* were found to be highly associated with those of the other soil dominant *Tranopelta* sp., which we believe to be a predator of the dominant and its mutualistic mealybugs.

Because of the modular nature of ant colonies (Andersen, 1991), worker populations vary more than do colony densities. These population fluctuations should be in response to resource availability, which should be strongly influenced by abiotic factors. Alternatively, population fluctuations could be due to interactions among members of the community, but probably still in response to resource availability. Ant communities are thought to be organized through competitive relationships (Fowler and Claver, 1991), and the occurrence of numerically dominant species necessarily limits resource availability for the remaining species of the community, as well as controls the upper limits of species numbers (Tilman, 1982).

Tropical ant communities have high faunal richness (Andersen, 1991). Of the 124 ground ant species recorded in a Bahian cocoa plantation, *Solenopsis* sp. A, *Wasmannia auropunctata* (Roger), *Solenopsis (Diplophoptrum)* sp. B, and *Carebarella* sp. were dominant in the litter stratum, and *Acropyga* cf. *paramaribensis* Borgmeier and *Tranopelta* sp. were dominants in the soil stratum (Delabie and Fowler, 1992). This strong dominance structure is not characteristic of tropical areas (Andersen, 1991), and the causes of these patterns are important components for an understanding of the organization of community structure (Tilman, 1982). The remaining ant species of these cryptic communities were collected only occasionally, and, thus, their importance in structuring these communities may be limited. Here, we address the following questions: [1] does weather have any relation to the population fluctuations of the dominant ant species?; and [2] do strong interactions exist among the dominant ant species? Either or both of these could produce changes in community structure.

METHODS AND MATERIALS

From June, 1986 to December, 1987, in an area of 0.83 ha on the Cocoa Research Station in Itabuna, Bahia, Brazil, 51 $15 \times 15 \times 15$ cm weekly soil samples were collected immediately below the litter layer. Each sample was taken 1.5 m from the trunk of one of 500 randomly chosen numbered trees. Ants were immediately extracted by hand sorting, and afterwards two successive sifters (2 and 1 mm mesh size) were used to extract ants not visually detected. Ants were preserved in 70% alcohol for subsequent identification in the laboratory.

Litter samples were collected at irregular intervals from February, 1987 to October, 1988, in the same experimental area, using the same sampling procedure. For each sample, a randomized 1 m² of litter near the trunk of a numbered tree was also collected, and its depth measured. These samples were extracted in a Berlese funnel for 48 hours, and then preserved in 70% alcohol and identified as in the soil samples.

For both soil and litter samples, we recorded species presence. Data were then transformed into percentages (number of samples per species/51 weekly samples). For both sampled strata, we compared only the dominant species, defined through species rank-abundance plots, using a criterion of 10% occurrence as a minimal value (Delabie and Fowler, 1992).

We correlated the weekly percentage of samples containing dominant species against data from the nearby Cocoa Research Center weather station. Data were smoothed by a 3 point moving average, and were then successively lagged for correlations. We regressed monthly percentage occurrence of the dominant soil species against each other.

RESULTS

Dominant litter species were *Solenopsis* sp. A (44.03%), *S. (Diplorhoptrum)* sp. B (13.82%), *W. auropunctata* (10.07%) and *Carebarella* sp. (10.07%), while for soil, dominant species were *A. cf. paramaribensis* (58.07%) and *Tranopelta* sp. (13.17%).

No significant correlations were found for any of the dominant species with temperature or precipitation (Fig. 1). However, a strong peak occurrence frequency of *Solenopsis* sp. A was evident at the end of the summer (April) (Fig. 1). The other dominant ant species showed no apparent seasonal trends (Fig. 1).

Similar comparisons were performed with the dominant soil species with leaf flush and climatic conditions (Fig. 2). After data smoothing, *A. cf. paramaribensis* percent occurrence was positively correlated with precipitation at a 5 week lag ($r = 0.60$; $P = 0.001$), while temperature and leaf flush were positively correlated with ant populations at a 12 week lag ($r = 0.52$; $P = 0.001$ and $r = 0.51$; $P = 0.001$, respectively).

By regressing the numbers of each of the two species per month for two species (Fig. 3), a strong relationship was found:

$$y = 0.33x - 2.88 \quad (r^2 = 0.64)$$

where y = percent of *A. cf. paramaribensis* in the monthly samples, and x = percent of *Tranopelta* observed in the samples during the same period.

DISCUSSION

Two of the dominant litter species are facultatively dependent upon honeydew (*W. auropunctata* and *Solenopsis* sp. A). *Carebarella* sp. and *S. (Diplorhoptrum)* sp.

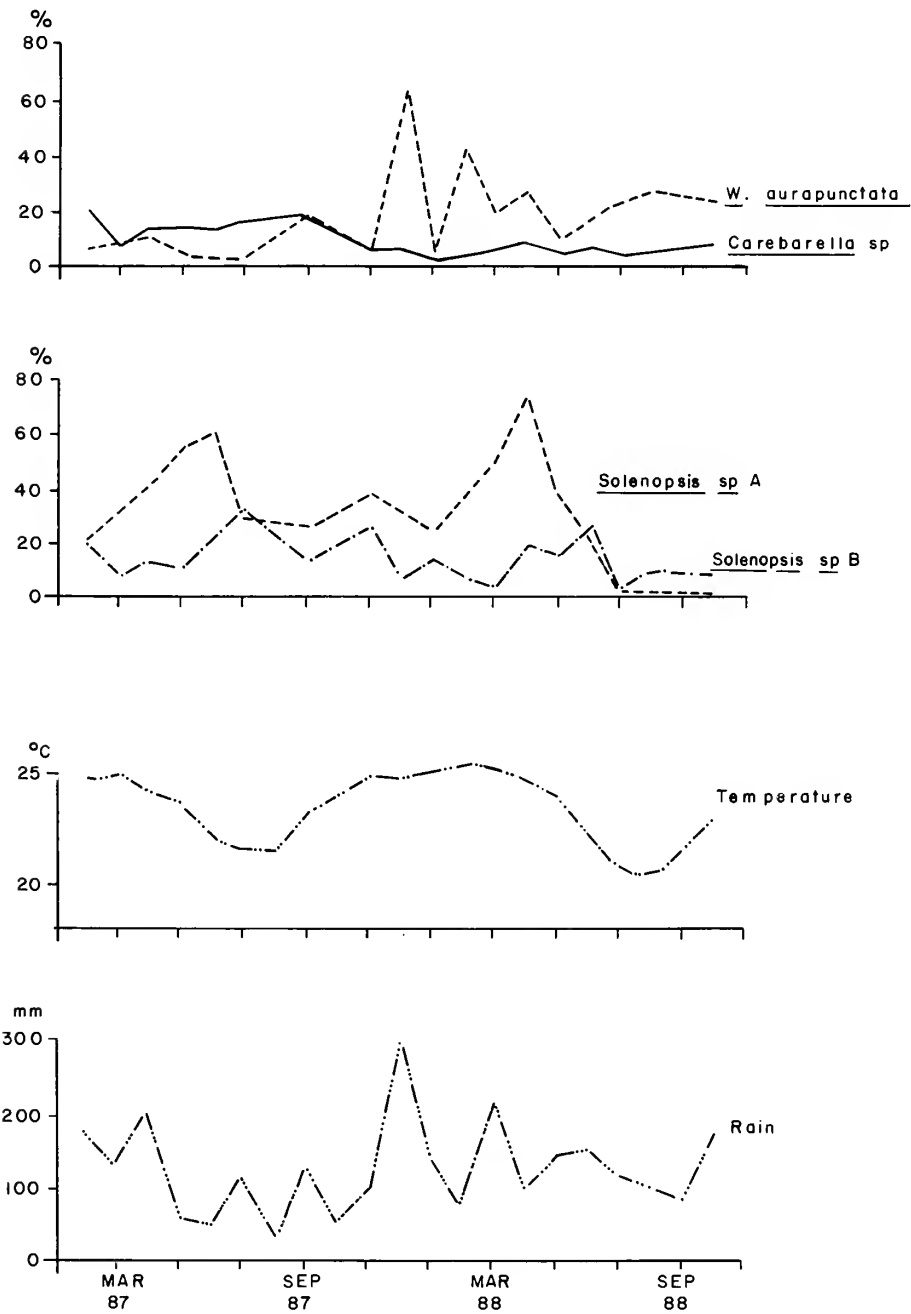


Fig. 1. Percent occurrence of the dominant ant species in Berlese litter samples over the study period, and corresponding air temperature and rainfall data.

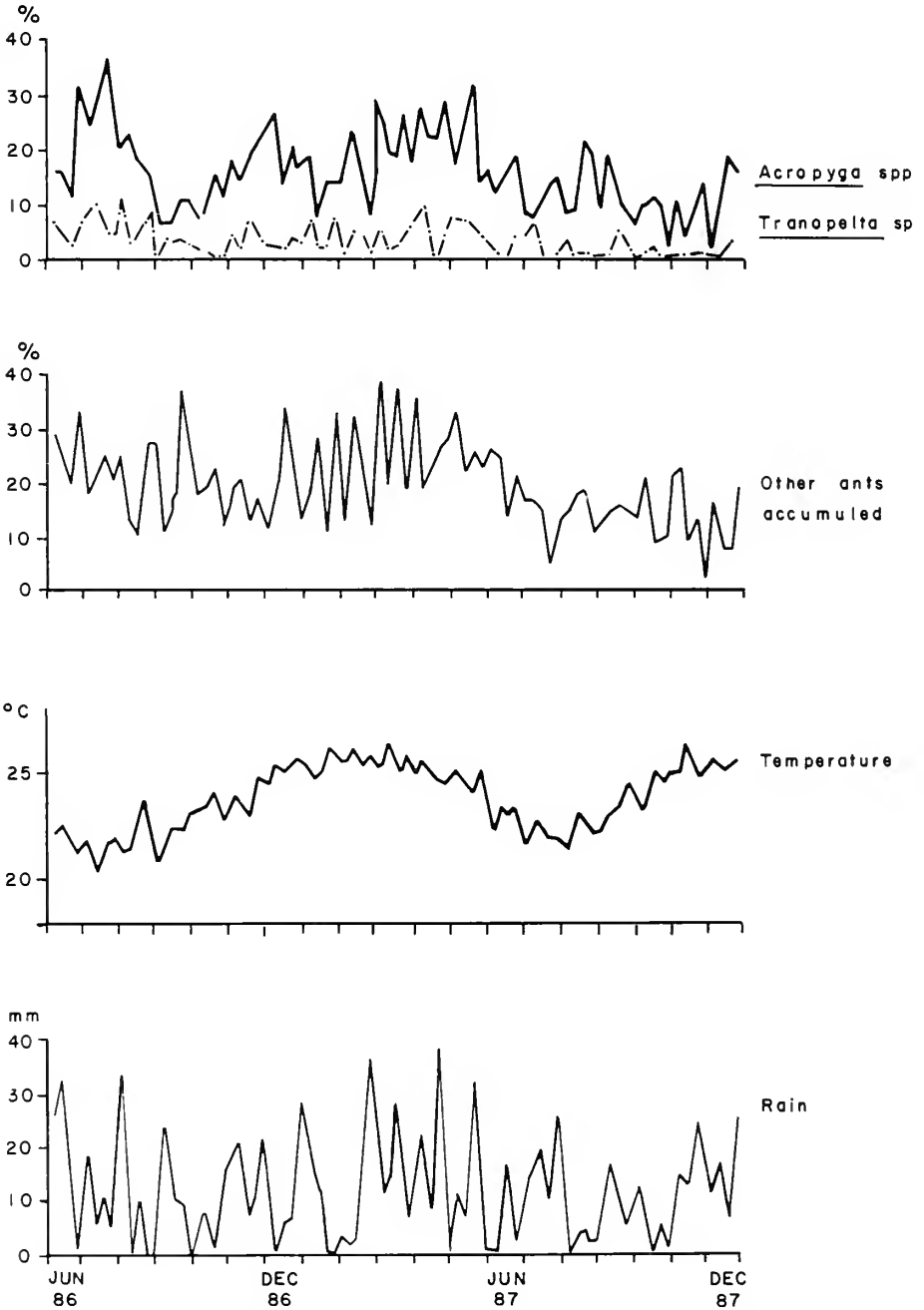


Fig. 2. Percent occurrence of the dominant ant species in soil samples over the study period, and corresponding air temperature and rainfall data.

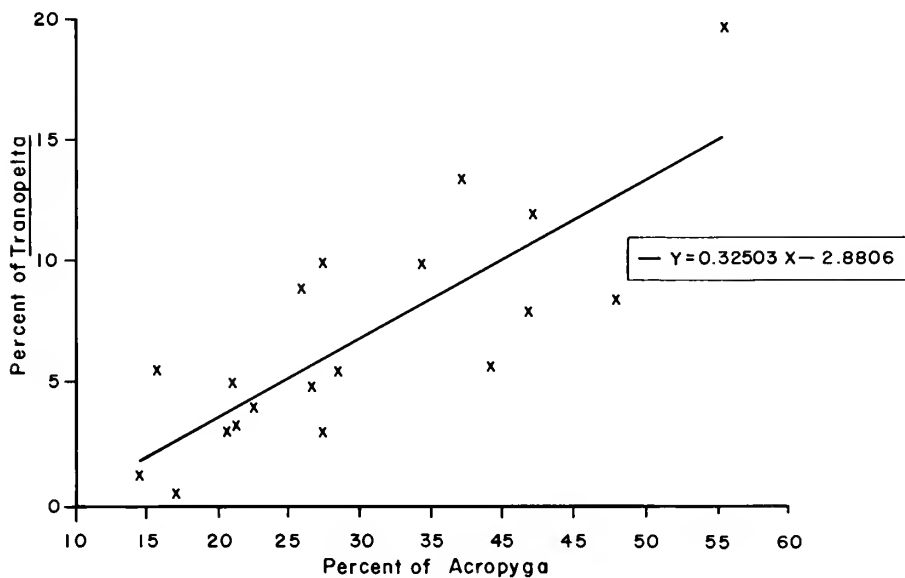


Fig. 3. The relation between the percent occurrence of the two dominant soil ant species over the sampling period.

B are both strictly carnivorous (Fowler et al., 1991), and foraging populations would depend on the type and abundance of prey present, which was apparently not directly influenced by climatic conditions.

We suggest that climate may indirectly influence the populations of *A. cf. paramaribensis* and its associated mealybugs. Climate influences both plant growth and leaf flushing, and we suspect that the mealybugs may have a greater physiological dependence upon the root's growth and turgor pressure, thus limiting the availability of food resources (Delabie et al., 1991). This may explain the 12 week lag in population response to temperature and leaf flush. The 5 week lag detected for population response to rainfall may indeed be an indication that humidity induces a quick population response of the associated mealybugs, and a corresponding increase of ant populations (Zanetti, 1992).

We have no information on the interrelations between *A. cf. paramaribensis* and *Tranopelta* sp. However, we suggest three possibilities to explain the positive correlations between population frequencies. The first possibility is that both depend upon mealybugs as a food resource. However, if mealybugs, or mealybug root substrate were limiting factors, this correlation should be negative to evidence competition. The second possible explanation is that *Tranopelta* preys upon *Acropyga*, but we have no evidence that this occurs. The data are, nevertheless, very reminiscent of typical predator behavioral functional responses. The third hypothesis is that both species are facultatively dependent, or that at least one species depends upon the other for either food or protection. This alternative was chosen in our regression model. *Tranopelta* sp. is a possible parent of the Solenopsidini tribe (Myrmicinae),

which is primarily predaceous, although some species will facultatively tend homopterans (Fowler et al., 1991). However, species of *Acropyga* (Formicinae) are entirely dependent upon root mealybugs as a food resource, forming one of the true mutualistic relationships among insects (Fowler et al., 1991). Therefore, we propose that *Tranopelta* may indeed protect colonies of *Acropyga*, and extract a tribute in either *Acropyga* workers or brood, or in symbiotic root mealybugs. Indeed, *Tranopelta* sp. is encountered much less than expected at both carbohydrate and protein subterranean baits (Fowler and Delabie, 1992), providing further indirect evidence for their facultative dependence. Obviously, controlled laboratory studies are needed to test these competing hypotheses.

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BOOK REVIEW

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The Development and Evolution of Butterfly Wing Patterns.—H. F. Nijhout. 1991. Smithsonian Institution Press, Washington and London. 297 pp. \$20 paper, \$45 cloth.

The variety of bright colors and intricate patterns on butterfly wings has probably kindled more careers in entomology and evolutionary biology than any other attribute of insect morphology. The vast numbers of butterflies in insect collections, the existence of commercial butterfly houses, and the drive to make a butterfly our national insect, all attest to butterflies' immense popularity. But, in addition to serving as the public relations poster children for the study of insects, the Papilionoidea have been of fundamental importance to biological research throughout history. Butterflies were influential to Darwin, Wallace, and Fisher in formulating their selection theories. More recently, research on butterflies has provided paradigms for such diverse fields as chemical ecology, coevolution, and Pleistocene refugium biogeography. A prescient H. W. Bates forecast in 1864 (as Nijhout quotes in his preface) that "the study of butterflies . . . will some day be valued as one of the most important branches of biological science."

Ironically, one area of butterfly biology that has received surprisingly little attention over the years is the evolution of the very wing patterns that attract so many people to study butterflies in the first place. In spite of the zealous naming of innumerable subspecies, races, variations, hybrids and aberrations on the basis of wing pattern variation, few synthetic studies of pattern evolution have been carried out. Those that exist have sunk into premature and undeserved obscurity. This book endeavors to reestablish the study of butterfly wings as a paradigm for evolutionary and developmental research.

In *The Development and Evolution of Butterfly Wing Patterns*, Nijhout resurrects classic studies by Schwanwitsch and Süffert from the 1920's, and synthesizes them with his own results into a relatively simple, comprehensive model of wing pattern development. The central premise of this model is that a homologous, ancestral pattern exists, the "nymphalid groundplan," from which the patterns of all nymphalids, and perhaps even of all Lepidoptera, can be derived. Nijhout presents his case clearly and thoroughly, building up from empirical results and the historical models to his own elaborate mechanistic hypothesis of wing pattern development. It is obviously essential to provide illustrations in a book about pattern evolution, and Nijhout succeeds admirably here. The book is profusely illustrated with figures reproduced from prior works, new half-tone photos and line drawings, and eight attractive color plates.

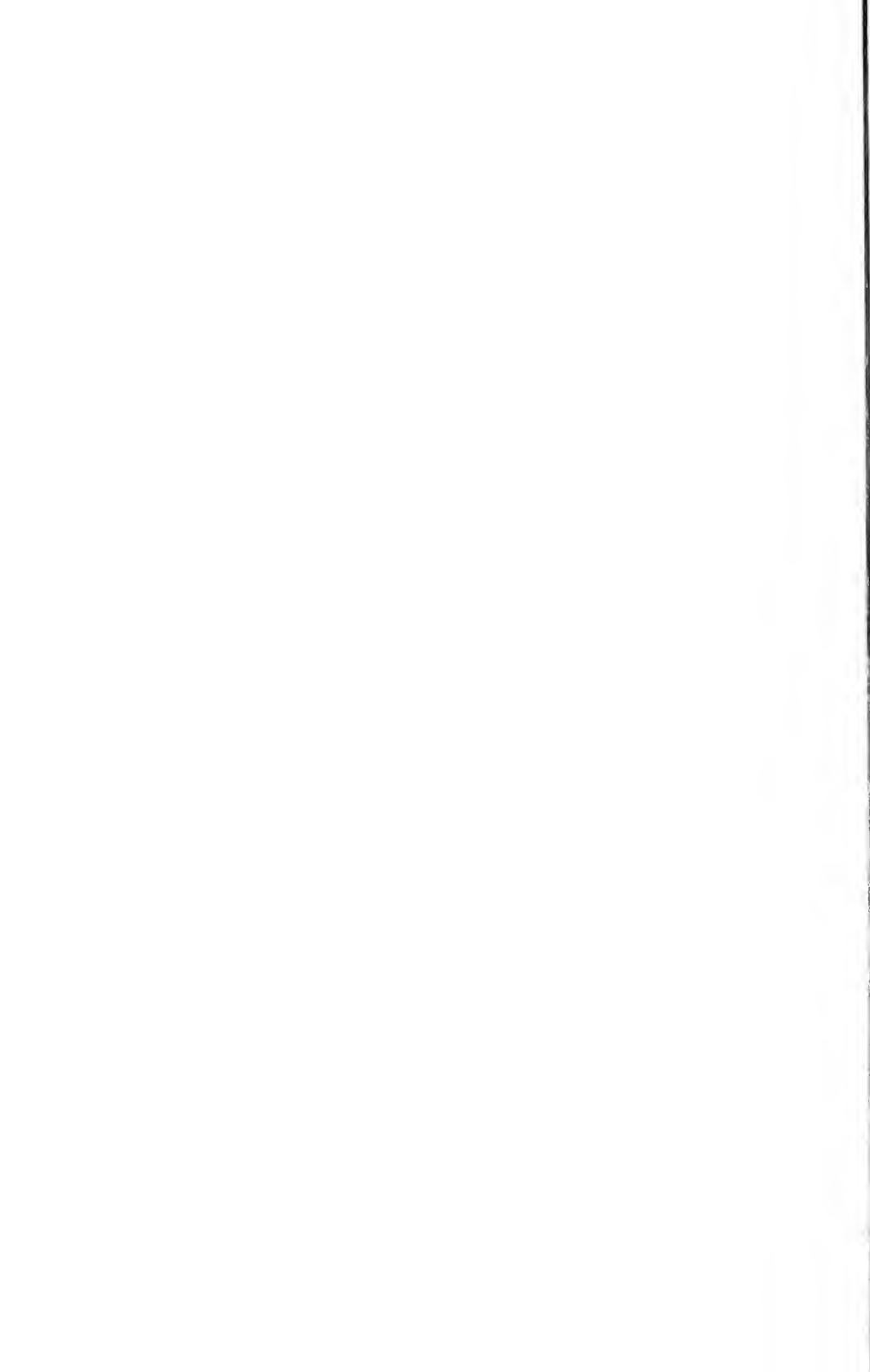
The first six chapters provide background and attempt to establish the orthodoxy of the wing-pattern developmental process. Chapter One introduces wing and scale morphological development, basic pigment chemistry and the critical idea of the wing as a static cellular monolayer. Chapters 2–4 lay out the Schwanwitsch-Süffert nymphalid groundplan concept and explore its themes and variations across a variety of intuitively problematical taxa, including the leaf butterfly, *Kallima inachus* (Nym-

phalidae: Nymphalinae), *Charaxes* (Nymphalidae: Charaxinae) and *Heliconius* (Nymphalidae: Heliconiinae). Nijhout argues that essentially any wing pattern can be homologized to the hypothetical groundplan, and further that serial pattern homology exists at several levels among wing cells and between fore and hindwings. Chapter Five presents experimental results which show that radical and complex changes in adult morphology can be produced by simple manipulations at precise developmental stages. Polymorphism, mimicry and polyphenism are discussed at length in Chapter Six, apparently to the end of demonstrating how these phenomena do not violate the general model, contrary to appearances. I suspect that most readers will find the 20-page explication of *Heliconius* wing-pattern genetics to be somewhat overwhelming.

The core of this book, Nijhout's model for pattern generation during development, is presented in Chapter Seven. The basic idea is that a set of static sources for a pattern-inducing signal are distributed in fixed positions across the wings. These points release the signal substance by diffusion at particular times during development. Patterns can evolve by the repositioning of these sources, and by shifts in timing or amount of signal production from a given source. Chapter Eight explores implications of the model, and suggests hypotheses for future research. An unexpected and valuable bonus to the book is the inclusion of two systematic appendices. The first presents recent phylogenies for major butterfly groups drawn from the literature, while the second is an important new cladistic classification of nymphalid subfamilies, tribes and genera by D. J. Harvey.

Nijhout presents his model of butterfly wing pattern evolution elegantly, carefully, and without any major flaws that I could detect. It is, in fact, difficult to envision any hypothetical wing pattern that could not be explained by his scheme. This is a mixed blessing, of sorts, because it reduces our interest in wing patterns as historical phenomena useful for systematics: all patterns become developmental homologs of one another and thus all apparent synapomorphies can be equally well-explained as parallelisms. The model implies that differences in wing patterns among taxa must be viewed as the phenotypic manifestation of recent selective forces for mimicry, sexual selection, crypsis, aposematism or other unidentified phenomena. On the other hand, the model also suggests that the genetic control of pattern formation is reasonably simple, depending more on differential local regulation of simple pattern-inducing substances than on complex arrays of pattern-producing "supergenes." If this is true, then perhaps some of Nijhout's hypotheses may soon be accessible to testing with molecular techniques, providing potentially enormous insights into the genotype-phenotype black box.

Although this book is fairly technical, and neither a desk reference nor a bedtime page-turner for the casual butterfly enthusiast, I found it to provide a novel, thought-provoking approach to the classic evolutionary problem of the development of complex features. In many respects, the book would be more sensibly shelved by subject, with other books on development, than by taxon, in the Lepidoptera section. The two-dimensional, static arrangement of cells in butterfly wings is a simple and tractable template for both theoretical and experimental manipulation in the study of development (reconfirming Bates' assertion that butterflies will become ever more important as model organisms across all branches of biology). That the resulting patterns also happen to be beautiful is serendipitous.—*Andrew V. Z. Brower, Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853.*



INSTRUCTIONS TO AUTHORS

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CONTENTS

A phylogenetic analysis and reclassification of the genera of the <i>Pococera</i> complex (Lepidoptera: Pyralidae: Epipaschiinae)	<i>M. Alma Solis</i>	1-83
New junior synonyms of <i>Frankliniella reticulata</i> and <i>F. simplex</i> (Thysanoptera: Thripidae)	<i>Sueo Nakahara</i>	84-87
Taxonomic and biological notes on North American species of <i>Elatophilus</i> Reuter (Hemiptera: Heteroptera: Anthocoridae)	<i>J. D. Lattin and N. L. Stanton</i>	88-94
A review of the genus <i>Melanocoris</i> Champion with remarks on distribution and host tree associations (Hemiptera: Heteroptera: Anthocoridae)	<i>J. D. Lattin and N. L. Stanton</i>	95-107
A key and diagnoses for males of the <i>incurvia</i> species-group of <i>Antiteuchus</i> Dallas with descriptions of three new species (Hemiptera: Pentatomidae: Discocephalinae)	<i>L. H. Rolston</i>	108-129
First record of Phrudinae (Hymenoptera: Ichneumonidae) from South America with notice of a new genus and species from Chile	<i>Charles C. Porter</i>	130-134
Physical and biotic correlates of population fluctuations of dominant soil and litter ant species (Hymenoptera: Formicidae) in Brazilian cocoa plantations	<i>Jacques H. C. Delabie and Harold G. Fowler</i>	135-140
Book Review		
The Development and Evolution of Butterfly Wing Patterns	<i>Andrew V. Z. Brower</i>	141-142